1987

Ecology of terricolous and corticolous bryophytes and lichens in relation to vascular plant communities and microclimate in central Iowa forests

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Order Number 8805090

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Iowa State University, 1987

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Ecology of terricolous and corticolous bryophytes and lichens in relation to vascular plant communities and microclimate in central Iowa forests

by

Cindy Lee Johnson-Groh

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Department: Botany
Major: Botany (Plant Ecology)

Approved:

Signature was redacted for privacy.

In Charge of Major Work

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For the Major Department

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For the Graduate College

Iowa State University
Ames, Iowa
1987

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PREFACE

"Children of lowly birth,
Pitfully weak;
Humblest creatures of the wood
To your peaceful brotherhood
Sweet the promise that was given
Like the dew from heaven:
'Blessed are the meek,
They shall inherit the earth';
Thus are the words fulfilled:
Over all the earth
Mosses find a home secure.
On the desolate mountain crest,
Avalanche-ploughed and tempest-tilled,
The sweet mosses rest;
On shadowy banks of streamlets pure,
Kissed by the cataracts shifting spray,
For the bird's small foot a soft highway
For the many and one distressed.
. . . . . .
Little sermon of peace."

Willis Boyd Allen

GENERAL INTRODUCTION

The relationship of terricolous and corticolous bryophytes and lichens to the surrounding vascular plant vegetation and microclimate poses complex ecological questions. Early investigators addressing these questions used primarily qualitative means, but recently quantitative analysis has permitted bryophyte ecologists to test the significance of their observations on ecological relationships. The present study was undertaken to compare quantitatively and qualitatively the bryophyte and lichen vegetation of deciduous forest communities in central Iowa and to attempt to elucidate relationships between the bryophytes, lichens, and vascular plant components.

Community plant ecology research has traditionally focused on the response patterns of vascular plants to complex environmental gradients. Bryophytes and lichens are usually neglected in such studies because of their quantitative insignificance, taxonomic challenge and sampling difficulties. While bryophytes and lichens in central Iowa may not constitute a dominant component of the vegetation, they are sensitive indicators of the microenvironment. Bryophytes, as indicators of special conditions, can aid in the evaluation of plant communities.

Goals of this study require quantitative data on the

vascular plants as well as the bryophytes and lichens, and the microenvironmental factors affecting bryophyte distributions. The vascular plant vegetation of the Ledges State Park was studied extensively (Johnson-Groh, 1983; Johnson-Groh, 1985; Johnson-Groh and Farrar, 1985). For this reason and because of its diversity of plant communities Ledges was chosen for this study. Permanent plots in which the vascular plants had been surveyed were used for this study, allowing direct comparisons of the bryophyte and lichen vegetation to vascular plant vegetation within the same plots. Results from the vascular plant survey (cited above) will not be detailed in this dissertation, except where necessary to understand relationships of bryophytes to vascular plants.

Of the vascular plant vegetation types described for Ledges (Johnson-Groh, 1985) only five of these (Quercus alba, Quercus alba-Quercus rubra, Quercus rubra, Quercus rubra-Tilia americana, Tilia americana types) were studied for their bryophytes and lichens. These types represent well defined upland woodland types with little evidence of recent disturbance and a well developed bryophyte and lichen component.

There are three portions of this study: microclimate observations, a survey of the terricolous bryophytes and lichens and a survey of the corticolous bryophytes and

lichens. The first section, microclimate observations, documents how the microclimate differs between slope aspects and thus between the major vascular plant vegetation types. Vascular plant distributions correlate closely with aspect. Because of the size of bryophytes and lichens their distributions may be expected to correlate even more closely with microclimate as influenced by topography.

The second section, terricolous bryophytes and lichens (ground-dwelling species) examines the distribution patterns and their relationships to vascular plants. The influence of the vascular plant community relative to that of the site (microclimate) on the distributions and abundances of bryophytes and lichens is examined.

The third section, corticolous bryophytes and lichens, (bark-dwelling species) examines the distribution of bryophytes and lichens relative to the vascular plant phorophyte (host tree), size, and community. The primary question addressed in this section is the differentiation of influence of the vascular plant community on bryophytes and lichens from the influence of phorophyte species. In other words, does the rare white oak in a basswood forest have the same mosses in the same quantities as the common white oak in a white oak forest?

SECTION I.

AN ANALYSIS OF MICROCLIMATE RELATIVE TO ASPECT AND PLANT DISTRIBUTIONS IN CENTRAL IOWA FORESTS

INTRODUCTION

Differences of microclimate account in part for different distributions of plants. An analysis of the microclimates resulting from slope aspect of Ledges State Park was undertaken to evaluate the effect microclimate has on the distribution of bryophytes. In a previous study (Johnson-Groh, 1985) at Ledges State Park bryophytes were shown to have a higher cover on north slopes than south slopes.

General Microclimate Studies

Previous studies have demonstrated large differences in microclimate within small geographic areas. Studies have primarily concentrated on the influence of the slope aspect and the degree of temperature and humidity moderation with height above the ground. Temperature, as a result of insolation-reradiation balance has been shown to be one of the major factors responsible for the differences in plant distributions (Rosenberg et al., 1983).

Many studies have documented the affect of slope aspect on temperature. In a very complete study of Cushetunk Mountain, New Jersey, Cantlon (1953) found that surface temperatures on south-facing aspects (hereinafter referred to as south slopes) were 1.1^{o} to 6.1^{o}C (2^{o} to 11^{o}F)

higher than north-facing slopes (hereinafter referred to as north slopes) in October. Potzger (1935, 1939) similarly found higher temperatures on south aspects in central Indiana. Shanks and Norris (1950) working in eastern Tennessee found a higher mean (1.6°C, 3°F) and higher maximum (6°C, 11°F) temperature on a south slope than on a north slope in the fall. Differences in minimum temperatures between aspects were usually less than .55°C (1°F). Shanks and Norris (1950) noted the importance of temperature maximum difference relative to freeze-thaw cycles, with south slopes thawing more frequently.

In a classical study of the Neotoma Valley in central Ohio, Wolfe et al. (1949) showed a considerable variation in the highest annual maximum surface temperature (24.4° to 58.8°C, 76° to 138°F) between woodland sites of different aspect. Minimum temperature extremes were 5°C (9°F) lower at one foot above the ground than at five feet. Cantlon (1953) found that the degree of difference in climate between slopes increased at the ground. On a south slope the average temperature at five centimeters was 3.3°C (6°F) higher than at one meter. On a north slope the average temperature at five centimeters was slightly cooler than the average temperature at one meter. Baum (1949) found temperatures near the ground to be cooler during the night and warmer during the day than higher above the ground. He

noted that these did not balance and resulted in a shift of mean daily temperature with height.

The development of a canopy reduces temperature differences between slope aspects. Wolfe et al. (1949) recorded the highest temperatures in spring before the canopy developed. Cantlon (1953) found the least difference between aspects in temperature (1.6°C, 3°F) in June when the canopy is fully developed and the angle of insolation is high. During the growing season, the temperature was 1.1°C (1.9°F) lower at five centimeters than at one meter on the south slope as opposed to 3.3°C (6°F) higher prior to canopy development. In areas of heavy shade, the temperature of north slopes was found to be significantly cooler at the surface than at one meter high. On the south slope, temperature at the surface was only slightly cooler than at one meter. Cantlon attributed these cooler surface temperatures to the interception of insolation and reradiation by vegetation. The minimum temperature was also found to be slightly higher at one meter than at the surface on both aspects.

Soil temperature has been studied less frequently. It is the surface and near surface temperatures which are of primary importance to plants. Bates (1923) looked at the vegetation on opposing slopes in the Rocky Mountains and found that the surface soil on the south slope was almost

33.3°C (60°F) higher than on the north slope. Wolfe et al. (1949) in central Ohio found the temperature below leaf litter seldom got below 0°C (32°F) and rarely above 25°C (77°F).

Atmospheric moisture has been studied through various methods and subsequent correlations have been made with plant water vapor loss. Because of the difficulty of measuring relative humidity and vapor pressure deficit at ground level, such measurements are subject to large errors. Likewise, evaporation from an open water saturated surface can not be directly correlated with losses of water vapor from the soil and plants. However, since evaporation rates from a surface are a function of the combined effects of air movement, air temperature, vapor pressure, insolation and temperature of the microsite surface, measured evaporation can give an approximation of water loss by plants in the same sites. Confirming this, Wolfe et al. (1949) found vapor pressure deficits, between leaf and air, to coincide with relative evaporation, from evaporimeters, in the same sites.

Using evaporimeters Potzger (1939) found evaporation to be consistently higher (up to 61%) on a south slope than on a north slope. Cantlon's results (1953) confirmed this difference, though his differences were smaller. Cantlon noted that absolute humidity decreases above the surface in

all sites. The vapor pressure deficit was found to be higher on the south slope and higher at one meter than five centimeters. Wolfe et al. (1949) showed that evaporation at soil level decreased up to 72% with the development of a canopy.

Soil moisture is less frequently reported by ecologists as a microclimate parameter and fewer studies have addressed its affects. Potzger (1939) reported that at six inches and at the surface there was a weekly average of 28% and 30% more moisture on the north slope than the south slope. Wolfe et al. (1949) noted that slow snow melt on the north slope accounted for more moisture and credited this as a factor in maintaining a moist well-decomposed leaf litter.

A more complete survey of the literature on the influence of slope aspect on the microclimate can be found in Cantlon (1953). Much of this literature is outdated and lacks quantitative data and so is not included here.

A few studies have presented microclimate data of very protected sites in order to explain distributions of specific plants. Farrar (1971) studied microclimates of protected rock outcrops in southern Illinois to explain the distribution of the independent gametophytes of Trichomanes as well as the sporophytes. Sites where the sporophytes existed were found to be more highly buffered from extremes in temperature than sites where only the gametophytes

occurred.

Peck (1980) studied the microclimate of a wooded canyon in central Iowa to explain distributions of mosses and ferns. He concluded that the microclimate moderation experienced at the bottom of the canyon has allowed the canyon to function as a refuge from the dry conditions of the uplands. He notes that the bryoflora is a sensitive indicator of the microclimate moderation. Fifty-four percent of the bryoflora found by Peck are at their western limit in Iowa and 15% of these are disjunct from eastern Iowa.

In an important study of endemic and disjunct moss species with tropical affinities in the southern Appalachian Mountains, Billings and Anderson (1966) investigated microclimate as a probable cause. They found the gorges where these mosses grew have seasonally reliable high amounts of rainfall with lower maximum temperatures and higher minimum temperatures than nearby sites. They concluded that these endemic and disjunct taxa were widespread prior to the Pleistocene and that during the Pleistocene they became restricted to these areas of equable microclimate.

Crum (1972) and Fulford (1951) noted the importance of microclimate in explaining the distributions of various taxa in current macroclimate regimes. Stotler (1976) noted that

50% of the species found in a canyon in southern Illinois have very restricted distributions which he attributed to differences in the microenvironment. He suggested that bryophytes in these protected canyons are not subject to extreme macroclimatic fluctuations and are relicts of once widespread distributions, their continued existence perpetuated by the microclimate.

Only a few studies have attempted to explain the local distribution of bryophytes on the basis of local variations in microclimate. Clausen (1952) characterized liverwort distribution in a heathland of Denmark. The number and density of species growing on a north-facing hillside was found to be greater than on the south-facing hillside. Clausen (1952, 1964) thought humidity was the greatest factor influencing the distribution of liverworts as reflected by their ability to withstand desiccation. Using Krogh's microclimatograph a change from 45% to 27% relative humidity was found from the ground surface on a south field up to one centimeter. A rather remarkable difference in relative humidity was found on one rotting log. Above Nardia scalaris the relative humidity was 85% while five centimeters away on a small protuberance the relative humidity above Frullania tamarisci was 55%.

Zehr (1977) looked at two mosses and three liverworts in three different sites and characterized their

microclimate. The vapor pressure deficit was found to be highest in the spring and lowest in the winter. It was lowest for Tricholea throughout the year. Leaf temperature and irradiance were found to reflect exposure of the site and were useful to compare the openness of the sites. Trichocolea, Nowelia and Lophocolea grow in more protected sites with less irradiance than do Atrichum or Diphyscium.

Van der Linden and Farrar (1983) looked at bryophyte distributions in tall-grass prairie relative to selected microclimate parameters. The found maximum summer surface temperature was higher on a southwest slope than a northeast-facing slope by 6.9°C. Likewise summer evaporation was 75.2% higher on the southwest-facing slope. The abundance of prairie species was strongly correlated with light intensity, especially with light intensities recorded in early evening.

Sholl and Ives (1973) studied the microclimate of Climacium americanum. They found that Climacium grows where there are relatively low maximum and minimum temperatures, high relative humidity and low evaporation. This study imparts little information on the factors controlling the distribution of Climacium relative to the distribution of other mosses, as the factors suitable for growth of Climacium appear suitable for most mosses.

Cantlon's study (1953) of microclimate included an

analysis of the bryoflora. He attributed the great differences in bryophytes (both cover and species) between slope aspects to the degree of difference in the microclimate. He maintained that the magnitude of difference between the bryophytes of the north and south slope is the most valid indicator of microclimatic differences.

In a follow-up study of Cantlon's work, Hamilton (1953) investigated the effect of slope on life forms of bryophytes. He found a greater number of life forms on the north slope than on the south slope. On the south slope only the compact (84%) and short turf (16%) growth forms were found whereas on the north slope, these growth forms represented only 48% and 22% respectively of the mosses present. Similarly Oosting (1942), using Raunkiaer (1934) life forms, (a system based on the position of the bud during the unfavorable season of the year: hemicryptophyte = buds at the surface, phanerophytes = buds raised above ground (least protected)) noted a predominance of cryptophytes on the north slope.

Iowa Microclimate Studies

Early studies of forest microclimate in Iowa include Bode's (1920) work at Backbone State Park. He stated that forest cover exerts a direct influence on evaporation.

Evaporation was greater at the tops of slopes than in the midslopes. Studies by Aikman comprise most of the forest microclimate work in Iowa. Working in Pammel Woods at Iowa State University, Dodge and Aikman (1932) found that forest cover lowered annual soil temperature compared to open areas. Also in Pammel Woods, Aikman and Smelser (1938) found the average annual air temperature was .55° to 1.1°C (1° to 2°F) lower in the maple-linden forest than in the oak hickory forest. They found lower midsummer evaporation in the maple-linden community (5.8 ml/day) than in the oak hickory community(8.9 ml/day). Soil moisture was highest on northly slopes where the soil temperature fluctuated the least.

The effect of slope aspect on climate was also assessed by Aikman (1941) in open unforested sites in western Iowa. Average monthly soil temperature at five centimeters was found to be coolest on the north slope (2°C, 78°C) and warmest on the west slope (29.9°C, 85.8°F). The greatest differences were found between the east and west slopes, which Aikman pointed out were not protected by nearby forest vegetation as were the north and south slopes.

Distributions of some native plants in Iowa have been attributed to microclimate. Aikman and Gilly (1948) noted, but did not quantify, the protected microclimate created by the Des Moines and Missouri Rivers and the subsequent

influence on the vegetation. Conard (1932a, 1932b, 1938, 1952) noted the northeastern distribution of boreal plants found on steep north slopes in Iowa is controlled by aspect and microclimate. Cooperrider (1962) found that 13% of the vascular plants on the north slope occurred on this aspect more frequently than other aspects.

Peck (1980) showed a large moderation of the microclimate from the prairie to the canyon of Woodman Hollow in central Iowa. He examined exposure, cover and temperature. The sites at the bottom of the canyon near the sandstone outcrops were found to have the highest cover, the lowest exposure to open sky and least daily variation in temperatures. Maximum temperatures at the bottom of the canyon on north sandstone ledges averaged annually approximately 18°C (32°F) cooler than temperatures on the south slope and approximately 28°C (50°F) cooler than the prairie.

A microclimate study of closed canopy sites versus open sparsely forested sites was conducted by Kucera (1952). The study sites for this work were located primarily in Ledges State Park and in pasture land surrounding the park. Temperature at twelve inches above the ground, soil temperature at one inch and soil moisture were monitored in addition to soil nutrients. Tables 1 and 2 contain a summary of Kucera's data for the closed canopy sites located

Table 1. Microenvironment data from Kucera (1952) for closed stands (upland and north slope) within Ledges State Park

	Upland			North
Stand No.	I	IV	X	V
Litter kg/ha	4603	5052	5389	2358
Duff kg/ha	11115	12013	11901	11901
Litter % moisture	59.7	83.0	80.5	71.5
Air Temp. at 30 cm, ^{o}C	29.7	28.8	28.0	28.0
Soil Temp. at 5 cm, ^{o}C	21.0	20.8	21.9	20.4
Evaporation mL/day	15.0	13.6	13.5	10.5
Soil Porosity % in top 5 cm	59.3	66.0	65.9	-
Total Nitrogen %	0.27	0.34	0.33	-
Organic Carbon %	3.5	4.2	3.4	-
pH	6.0	5.7	6.4	-

Table 2. Microenvironment data from Kucera (1952) for closed stands (south and east slopes) within Ledges State Park

	South		East	
Stand No.	II	XIV	IX	XII
Litter kg/ha	3556	3368	2807	2807
Duff kg/ha	14932	12575	9880	11789
Litter % moisture	30.1	59.1	30.9	53.0
Air Temp. at 30 cm, ^{o}C	28.6	28.2	28.0	-
Soil Temp. at 5 cm, ^{o}C	21.5	22.2	21.3	-
Evaporation mL/day	12.9	13.4	11.6	-
Soil Porosity % in top 5 cm	-	63.7	62.7	50.0
Total Nitrogen %	-	0.23	0.35	0.23
Organic Carbon %	-	2.8	4.0	3.4
pH	-	6.5	6.7	5.8

inside the park boundaries. He found that forest cover lowered soil temperature 5.5° to 8,3°C (10° to 15° F) and air temperature 2.2° to 4.4°C (4° to 8°F) in closed forest sites compared to open sites. There was nine percent more available moisture in closed sites during the winter because of greater snow accumulation. At no time did soil moisture become unavailable in closed canopy sites, but it dropped below the wilting point in open woods.

Kucera noted that canopy development as well as litter cover reduced summer soil temperatures. Midafternoon summer soil surface temperatures were 5.5° to 5.3°C (10° to 15°F) cooler than air temperature if there was sufficient litter cover. With sparse litter cover the soil temperature often exceeded the air temperature. This was especially true on south aspects. The lowest evaporation was found under the most dense canopies. Ash, calcium, and magnesium were lower for white and red oak litter than for maple basswood litter.

These studies of microclimate show the influence of temperature and evaporation on the localized distributions of plants to be significant. The affect of slope aspect on the microclimate results in large temperature and soil moisture differences which presumably control the distributions of plants. In order to adequately explain the differences in species distributions, the differences in microclimate must be accounted for also.

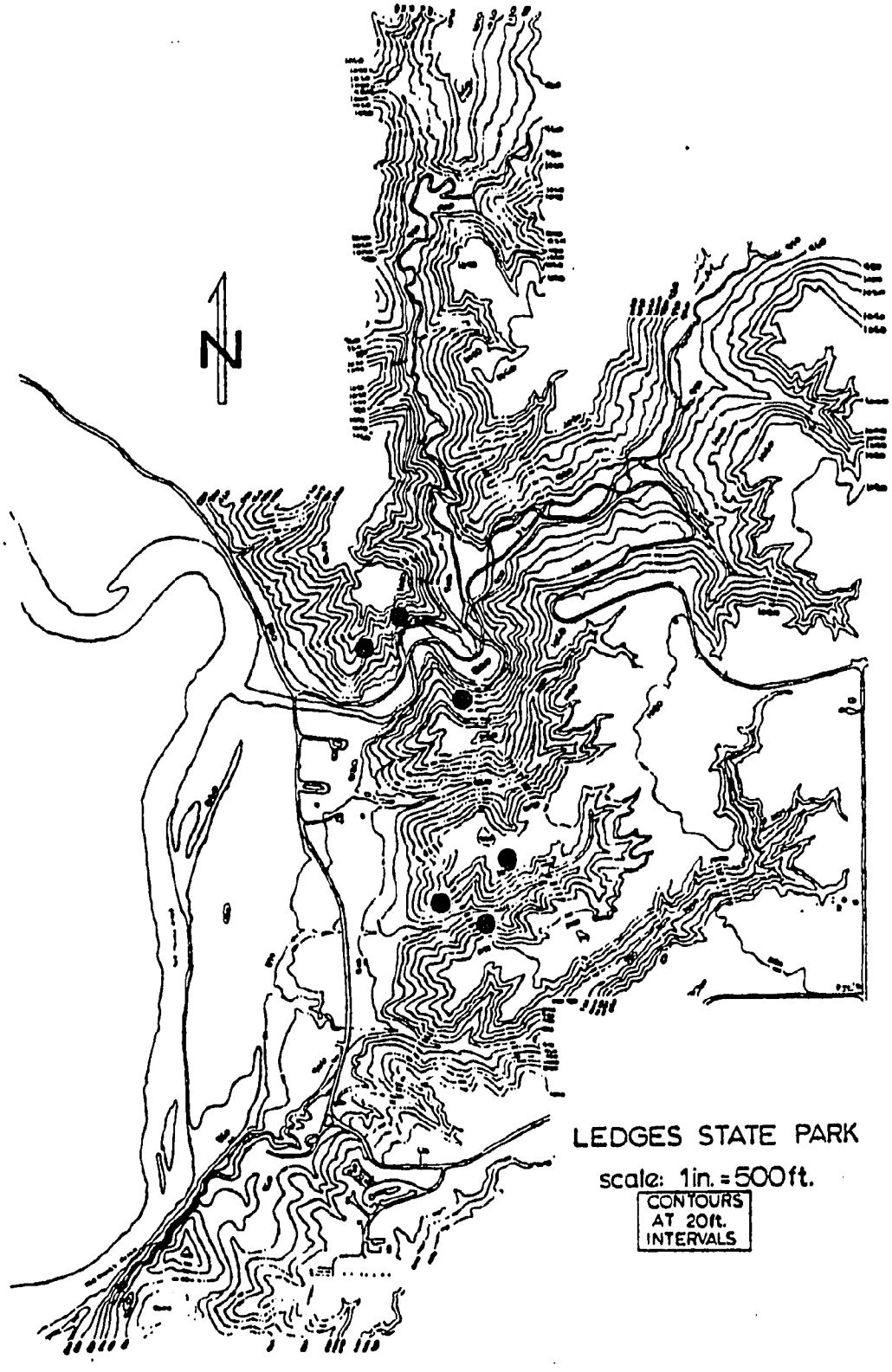
METHODS

Three parameters of microclimate were selected for study: maximum and minimum temperature, evaporation, and soil moisture. Each of these was monitored in six sites within Ledges State Park. The six sites were chosen from the 53 plots (50 x 20m) surveyed by Johnson-Groh (1983) to represent north and south slopes and flat uplands (Figure 1). These sites were also part of the bryophyte ground and epiphyte survey. Care was taken to locate the sites within easy waking distance to minimize time differences between observations.

At each of the sites two Six's maximum-minimum thermometers were placed approximately ten meters in from the ends of the plots along the centerline. (Figure 2). The thermometers were placed on the ground near mosses and covered lightly with litter to prevent direct exposure to solar radiation. Thermometers were placed under full canopies without canopy gaps. At these same locations Bouyoucous soil moisture blocks were buried five centimeters below the soil surface to measure soil moisture conditions influencing the mosses. Bouyoucous blocks were used because this method allows repeated sampling of the same point.

One evaporimeter was placed in the center of each of the six plots. The evaporimeter consisted of the outer

Figure 1. Location of microclimate study site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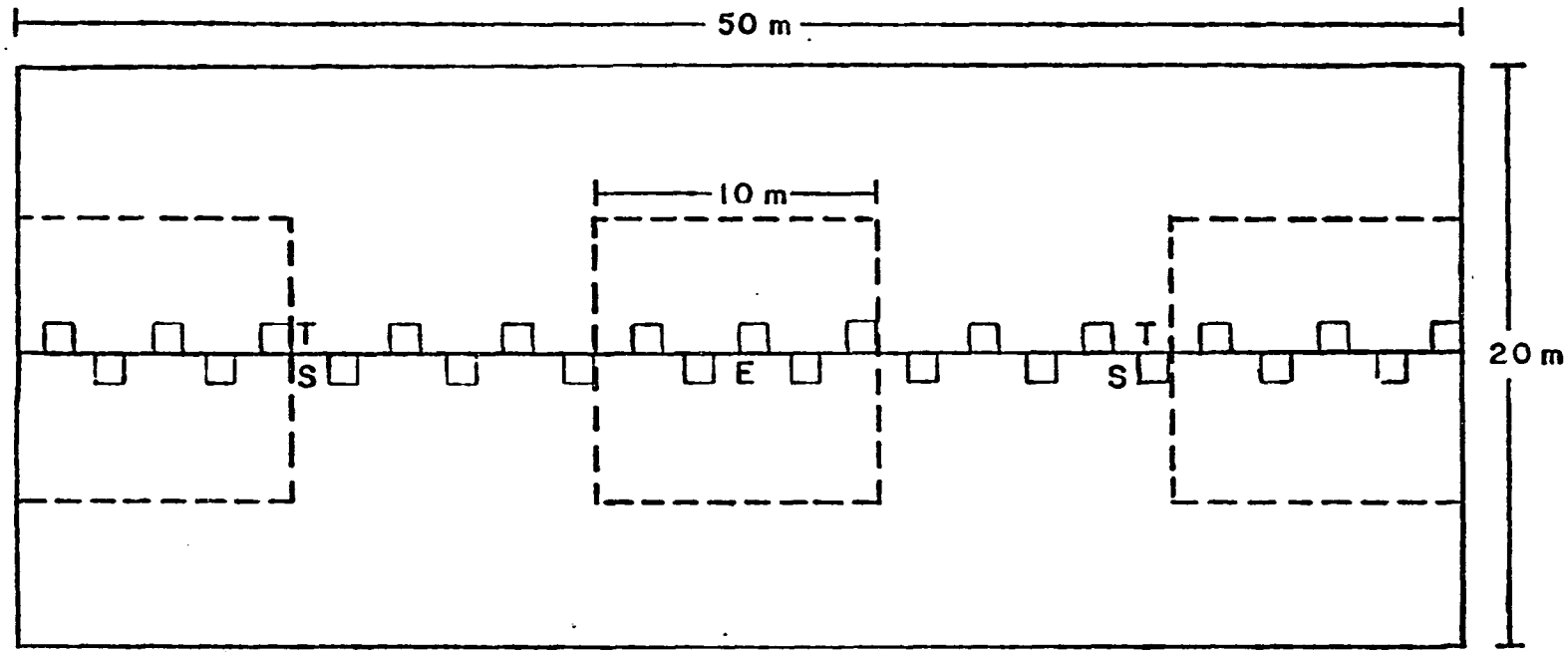
LEDGES STATE PARK
scale: 1in. = 500ft.
CONTOURS AT 20ft. INTERVALS

Figure 2. Location of thermometers, soil moisture blocks and the evaporimeter within the plot



E= Evaporimeter

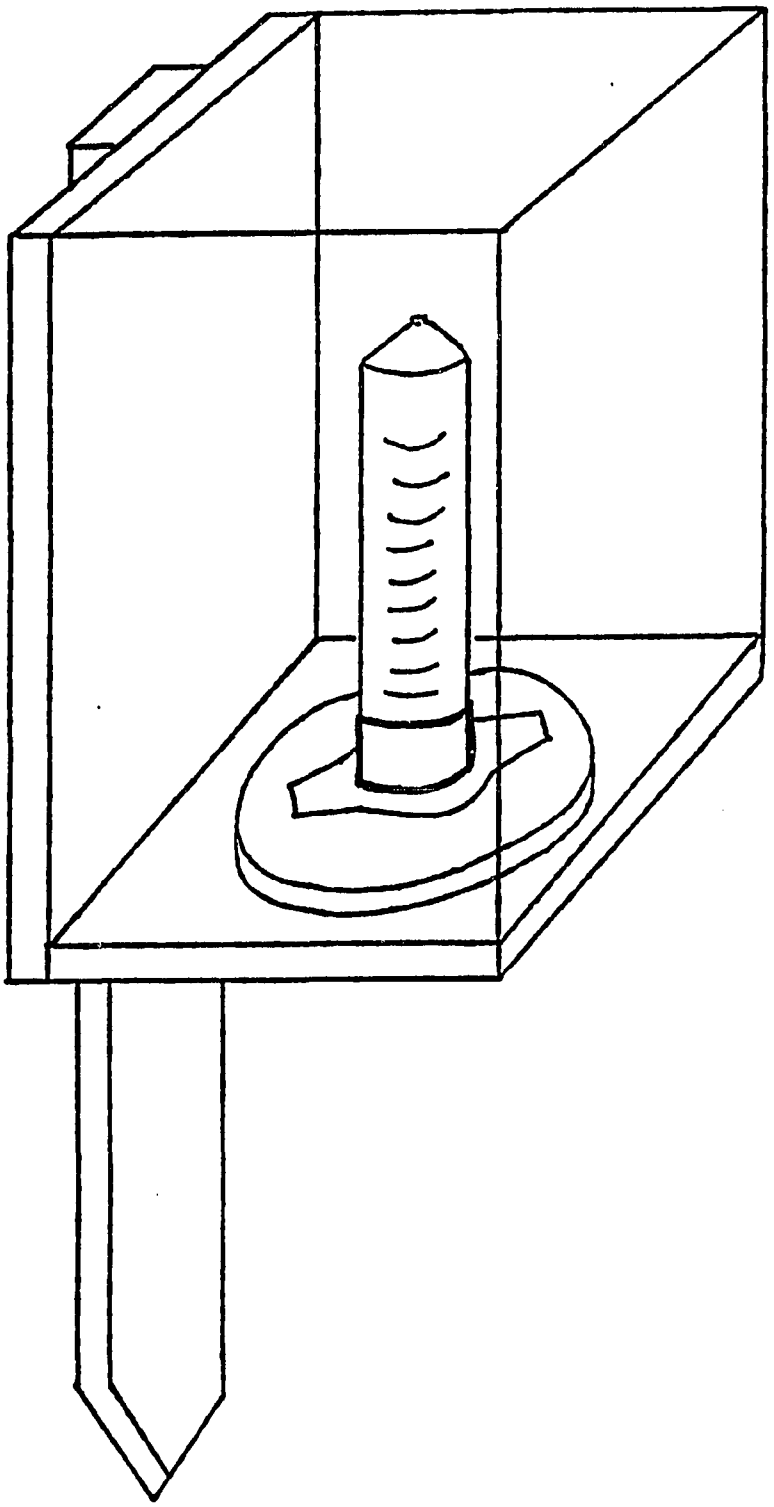
S= Soil Moisture Block

T= Thermometer

portion of a calibrated plastic syringe which had been sealed at the narrow end. This was filled with water and inverted on a petri dish covered with a filter paper (Figure 3). The syringe was stabilized by a piece of lead wrapped around its base. Evaporation from the free surface of the filter paper was recorded as the water receded in the syringe. The evaporimeter was placed in a box which consisted of hardware cloth on four sides and wood on the bottom and on one side. The box was anchored to a stake driven into the soil. It is possible that the box influences evaporation. To hold this influence constant the wood side of the box was always placed to face south. These boxes were effective in keeping the evaporimeters from being tipped over.

Temperature was monitored monthly prior to the development of the leaf canopy from November 1984 until April 1985 and after the canopy was lost from October 1985 through November 1985. During the growing season, temperature, soil moisture and evaporation were monitored approximately twice each week. Macroclimate data on temperature and precipitation from Boone, Iowa, 8 km north of Ledges State Park, were obtained from Climatological Data (1984-1985).

Figure 3. Diagram of an evaporimeter



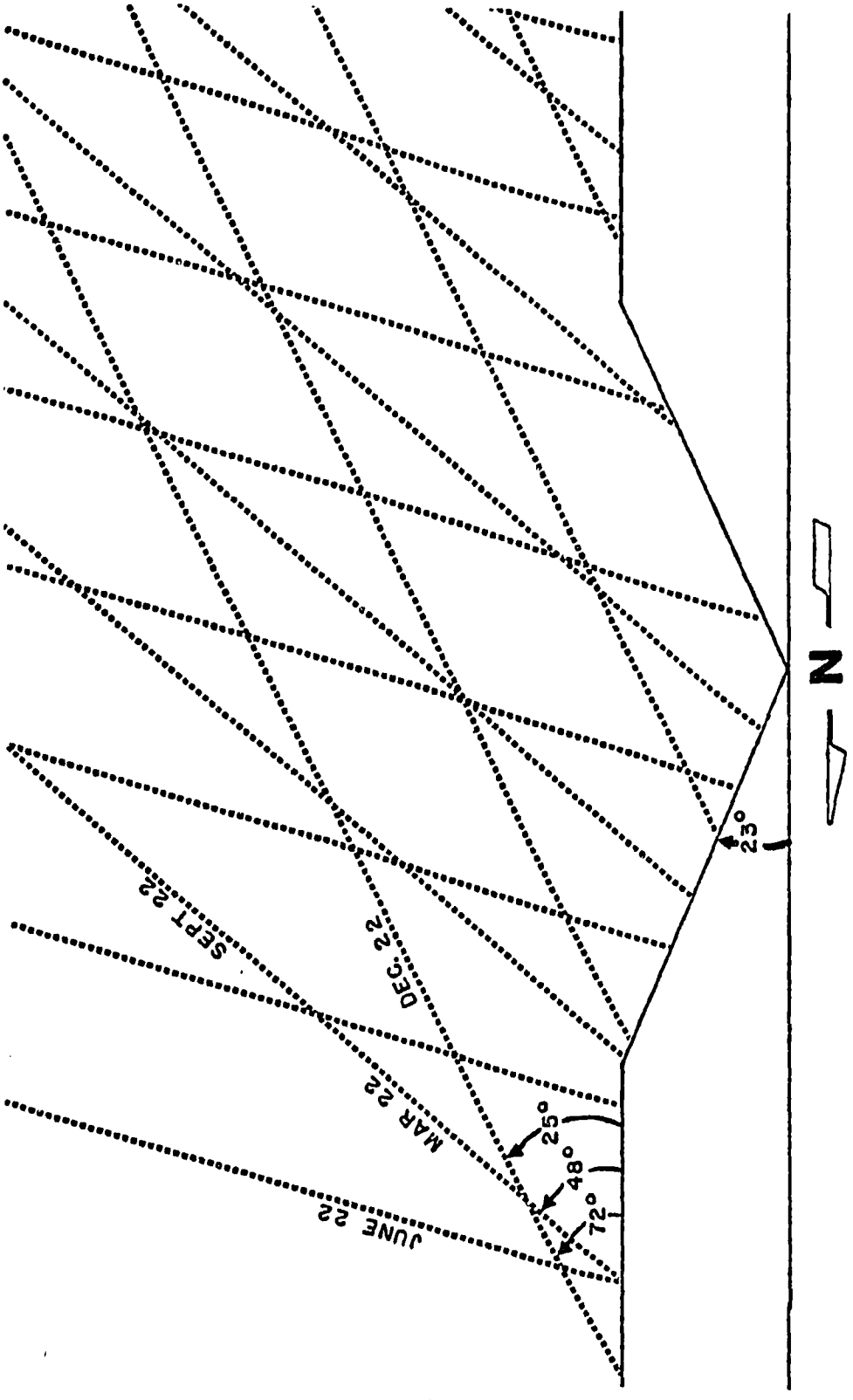
RESULTS AND DISCUSSION

Insolation

Differences in microclimate between slopes of different aspects are primarily due to insolation differences. A model can be constructed which shows the difference in the seasonal insolation on north and south slopes. Figure 4 shows the angle of incidence at noon for December 22, March 22, June 22, and September 22. Solar altitudes were calculated for Ames at 42° latitude and $93^{\circ}39'$ longitude (Frank and Lee, 1966; Fons et al., 1960). The average angle of slope inclination at the Ledges is 23°.

A large difference is apparent in this model. South slopes receive much more direct insolation during the spring and fall than does the north slope. The direct radiation received on March 22 can be calculated to further exemplify the difference. Assuming a value of 768 watts/m^2 for direct radiation on a surface normal to radiation on March 22, the direct radiation on a north slope of 23° is 321 watts/m^2 on a south slope of 23°, 726 watts/m^2 are received. This large difference in insolation creates subsequent differences in temperature, evaporation and soil moisture. There is less difference in radiation received between slopes during the summer due to the high angle of incidence. In summer the south slope receives 1.12 langleys/min, the north slope

Figure 4. Diagram of seasonal insolation received on north- and south-facing slopes in Ames, Iowa


N
23°
25°
48°
72°
JUNE 22
MAR 22
DEC 22
SEPT 22

receives .99 langleys/min. Differences at ground level are further modified in summer by presence of tree canopy.

Temperature

North slopes had consistently cooler maximum temperatures than either the south slopes or the upland (Figures 5, 6). In absence of a full leaf canopy (prior to May 2, and after October 15) the average monthly maximum temperature of the north slope was 14.1°C (57.4°F). On the south slope and upland the average monthly maximum temperature in the absence of canopy was 22.5°C (72.5°F) and 20.0°C (67.8°F) respectively. The monthly average difference between the north and south slope in the absence of canopy is 8.4°C (15.1°F). There is less difference, 2.6°C (4.7°F), between the south aspect and the upland because of the relatively steep angle of insolation for both aspects.

After full canopy development the differences are smaller. The north slope monthly average maximum temperature with canopy was 23.1°C (73.5°F), the south slope was 25.5°C (77.9°F) and the upland was 25.0°C (77.0°F). The average difference between the north and south slopes was 2.4°C (4.4°F). This smaller difference results from two factors. First the angle of incidence is higher and so more radiation is received on the north slope. Secondly the

Figure 5. Maximum temperatures for south- and north-facing slopes based on an average of four thermometers in two plots on each aspect

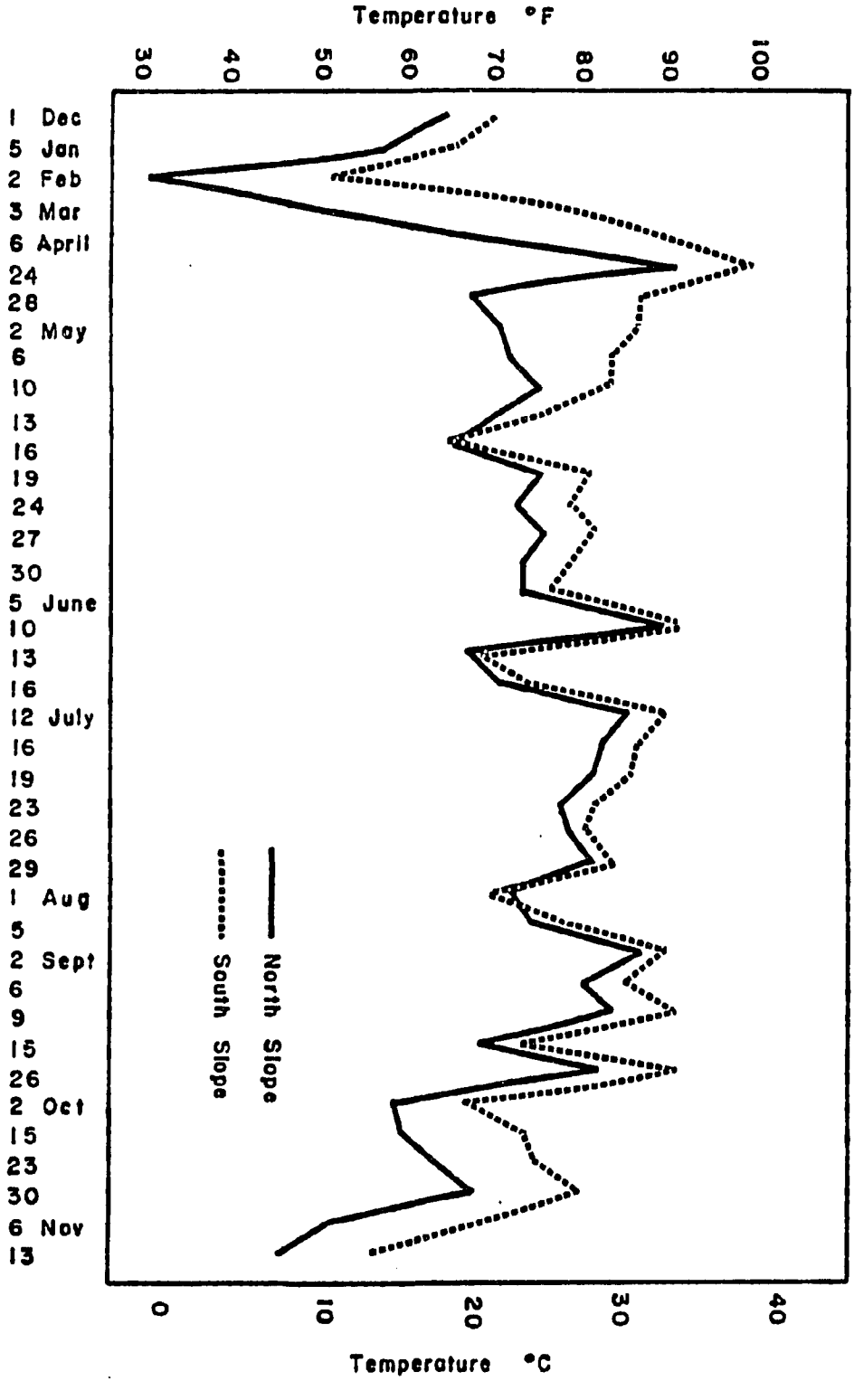
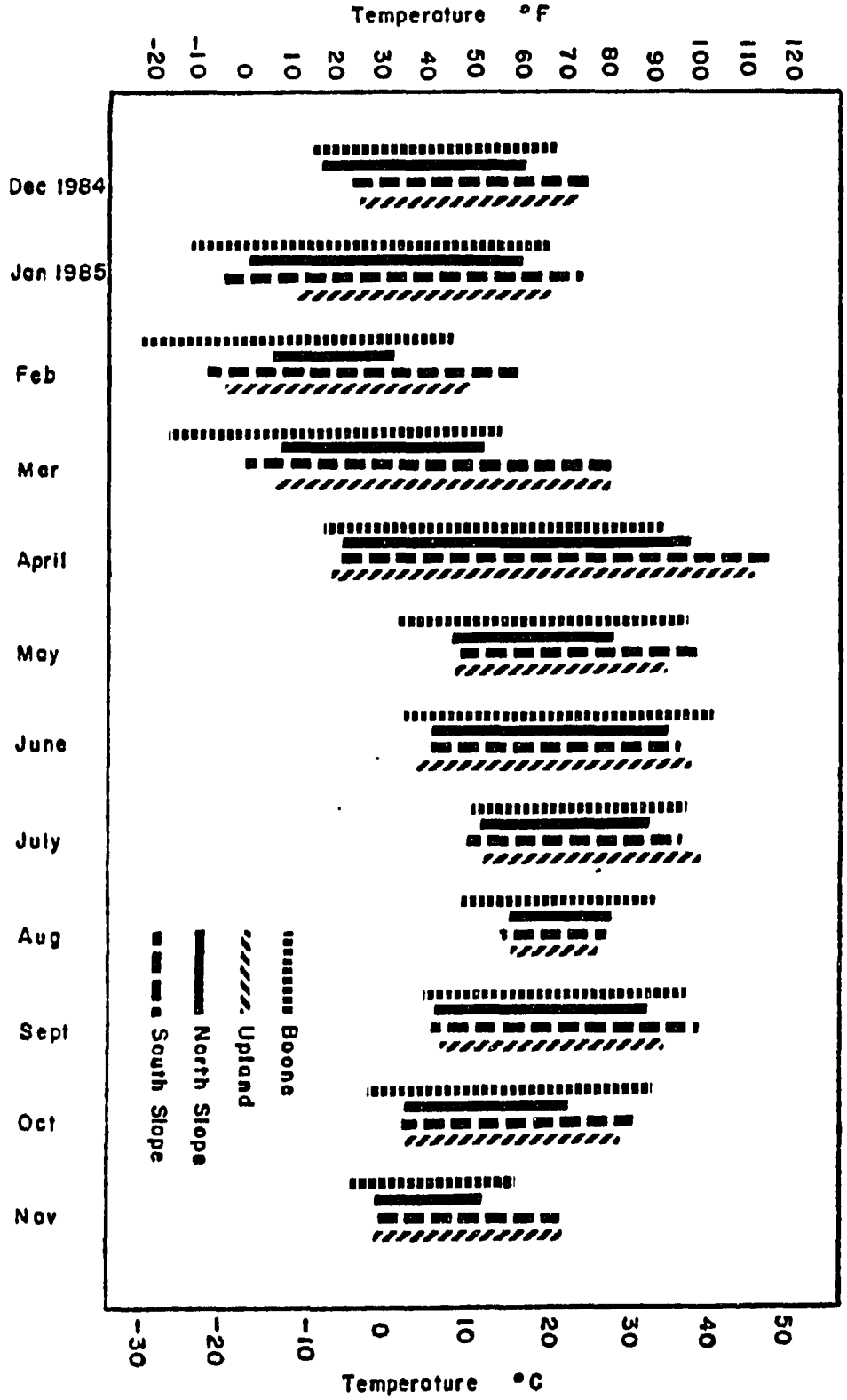

Temperature °F
30
40
50
60
70
80
90
100
1 Dec
5 Jan
2 Feb
3 Mar
6 April
24
28
2 May
6
10
13
16
19
24
27
30
5 June
10
13
16
12 July
16
19
23
26
29
1 Aug
5
2 Sept
6
9
15
26
2 Oct
15
23
30
6 Nov
13
North Slope
South Slope
0
10
20
30
40
Temperature °C

Figure 6. Range of temperature for south- and north-facing slopes. Averages of four thermometers in two plots on each aspect


Temperature °F
-20
-10
0
10
20
30
40
50
60
70
80
90
100
110
120
Dec 1984
Jan 1985
Feb
Mar
April
May
June
July
Aug
Sept
Oct
Nov
South Slope
North Slope
Upland
Boone
-30
-20
-10
0
10
20
30
40
50
Temperature °C

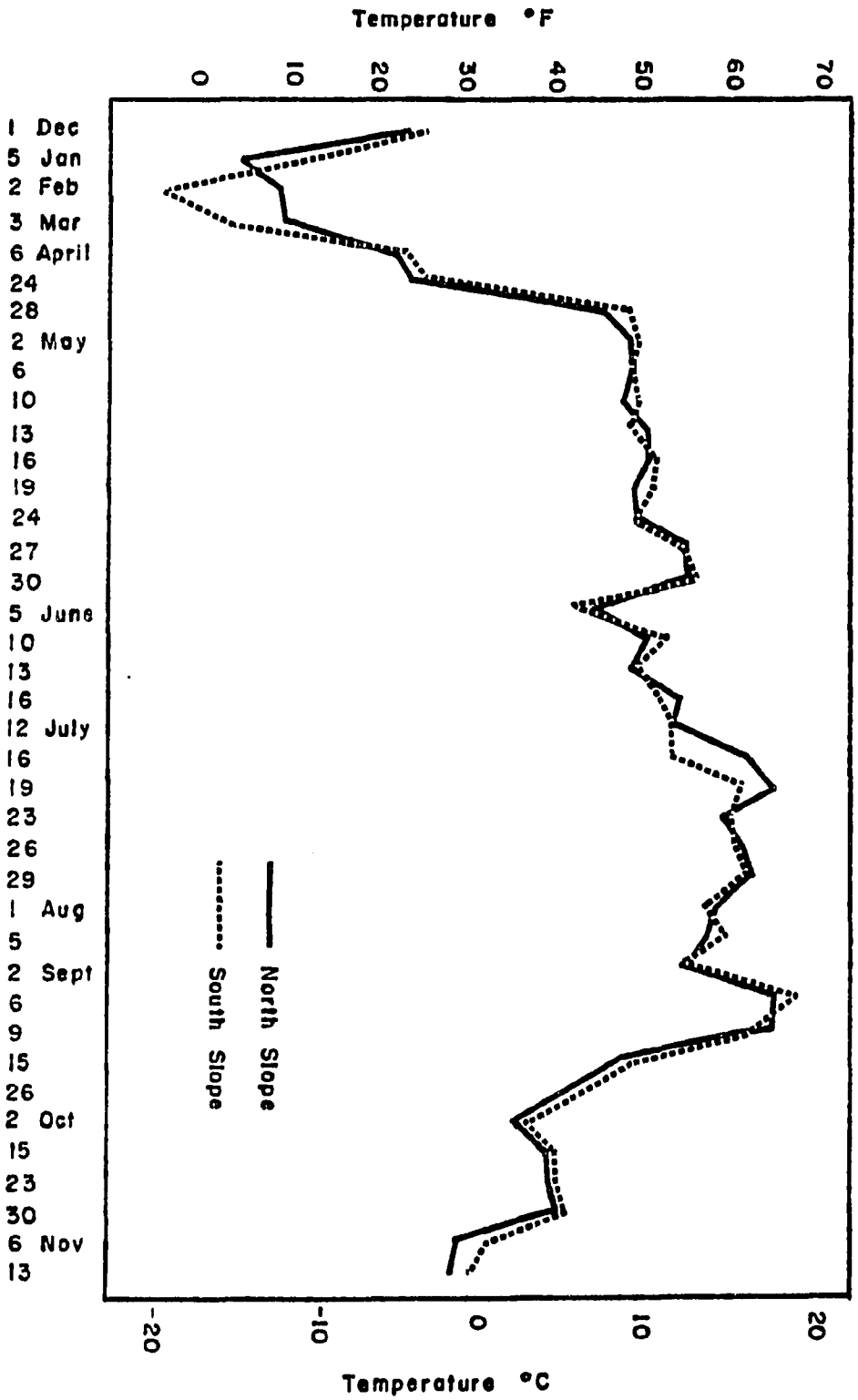
radiation is intercepted by the canopy so that little direct radiation reaches the ground. For the same reasons, the difference between the upland and south slope is insignificant (.5°C, .9°F). The monthly average difference throughout the year (with and without canopy) between the north and south slope was 5.8°C (10.4°F).

Minimum temperatures were not significantly different between north and south slopes (Figures 6, 7). The monthly average minimum temperature in absence of canopy on the north slope was -4.3°C (24.3°F), on the south slope -4.8°C (23.4°F), and on the upland -2.6°C (27.3°F). With canopy the monthly average minimum temperature on the north slope was 10.8°C (51.5°F), on the south slope 11.0°C (51.8°F), and on the upland 11.3°C (52.4°F). Little difference in minimum temperatures is expected since all areas were equally forested and reradiation from each would be comparable.

North slopes are moderated from extremes of temperature (Figure 6). They consistently reach lower maximum temperatures during the day than south slopes and uplands. Thus the area climate temperature data (from Boone) does not adequately express the microclimate variation present in the canyons of Ledges State Park.

The south slopes presumably undergo significantly more freeze-thaw cycles due to their wider range of temperatures in late fall and early spring. North slopes retained snow

Figure 7. Minimum temperature for north- and south-facing slopes based on an average of four thermometers in two plots on each aspect


Temperature °F
0
10
20
30
40
50
60
70
1 Dec
5 Jan
2 Feb
3 Mar
6 April
24
28
2 May
6
10
13
16
19
24
27
30
5 June
10
13
16
12 July
16
19
23
26
29
1 Aug
5
2 Sept
6
9
15
26
2 Oct
15
23
30
6 Nov
13
North Slope
South Slope
-20
-10
0
10
20
Temperature °C

for a longer period in the spring, and frequently the soil there was frozen while the soil on south slopes was warm and dry.

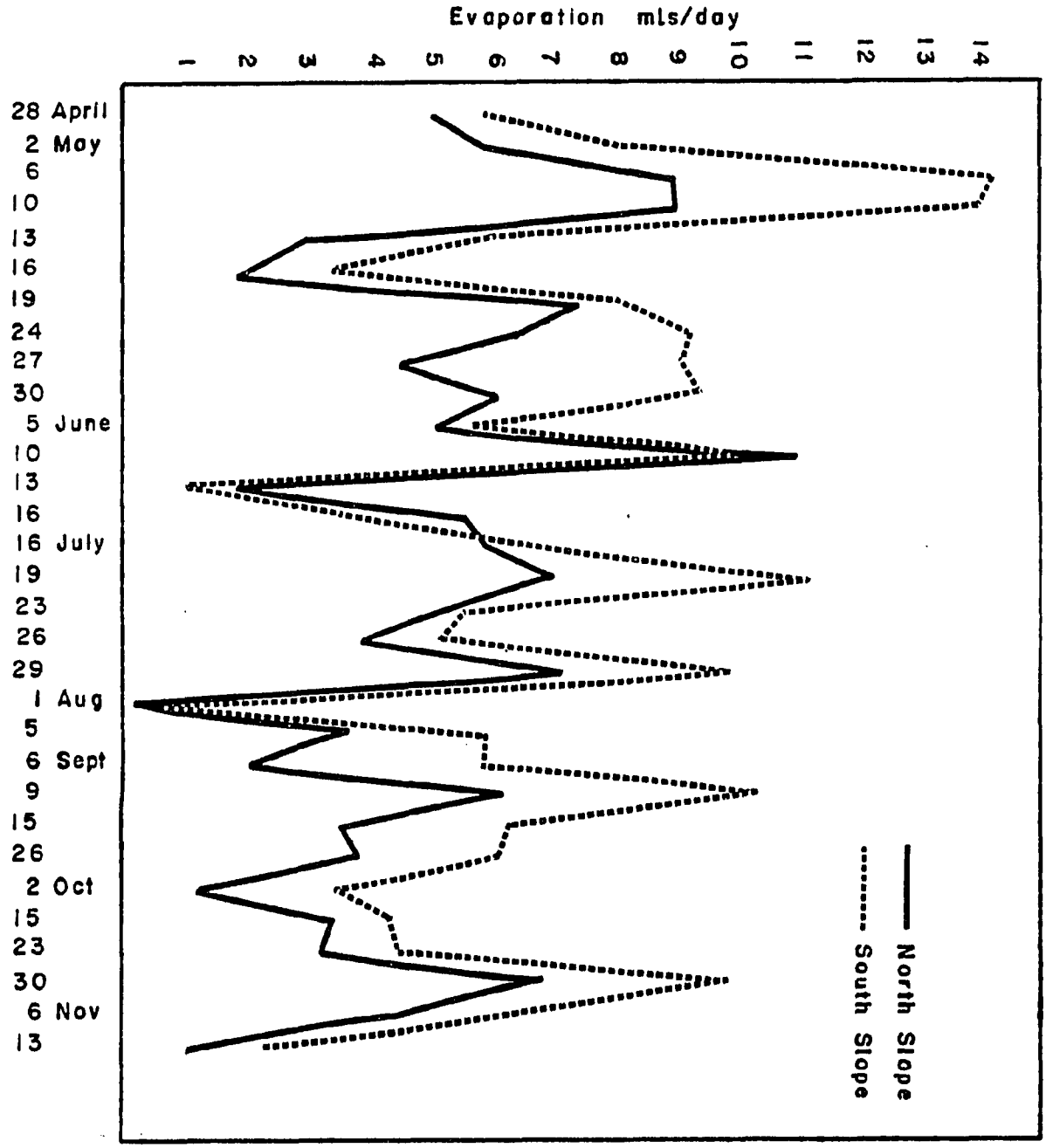
Evaporation

Evaporation from evaporimeters approximates potential evaporation from a free water surface. Although this can not be equated to actual losses of water from the soil or from plants, it does give an estimate of the relative potential evaporation of a particular site, which will vary with air movement, air temperature, vapor pressure and insolation.

The north slope had consistently lower evaporation than did the south slope (Figure 8). In absence of tree canopy (from April 28 to May 2 and October 23 to November 13) the north slope evaporimeters lost an average of 4.7 ml/day, while on the south slope and the upland, 6.4 ml/day and 6.0 ml/day respectively were lost daily. With canopy present, 4.4 ml/day were lost from evaporimeters on the north slope, 6.1 ml/day on the south slope and 5.8 ml/day on the upland.

The higher rates of evaporation (40%) on south slopes are consistent with the higher temperatures found on the south slopes. The overall higher rates during the period of canopy presences are thought to be due to higher temperatures of summer. It should be noted though that the

Figure 8. Free water evaporation for north- and south-facing slopes based on an average of two evaporimeters in two plots on each aspect


Evaporation mls/day
1
2
3
4
5
6
7
8
9
10
11
12
13
14
28 April
2 May
6
10
13
16
19
24
27
30
5 June
10
13
16
16 July
19
23
26
29
1 Aug
5
6 Sept
9
15
26
2 Oct
15
23
30
6 Nov
13
North Slope
South Slope

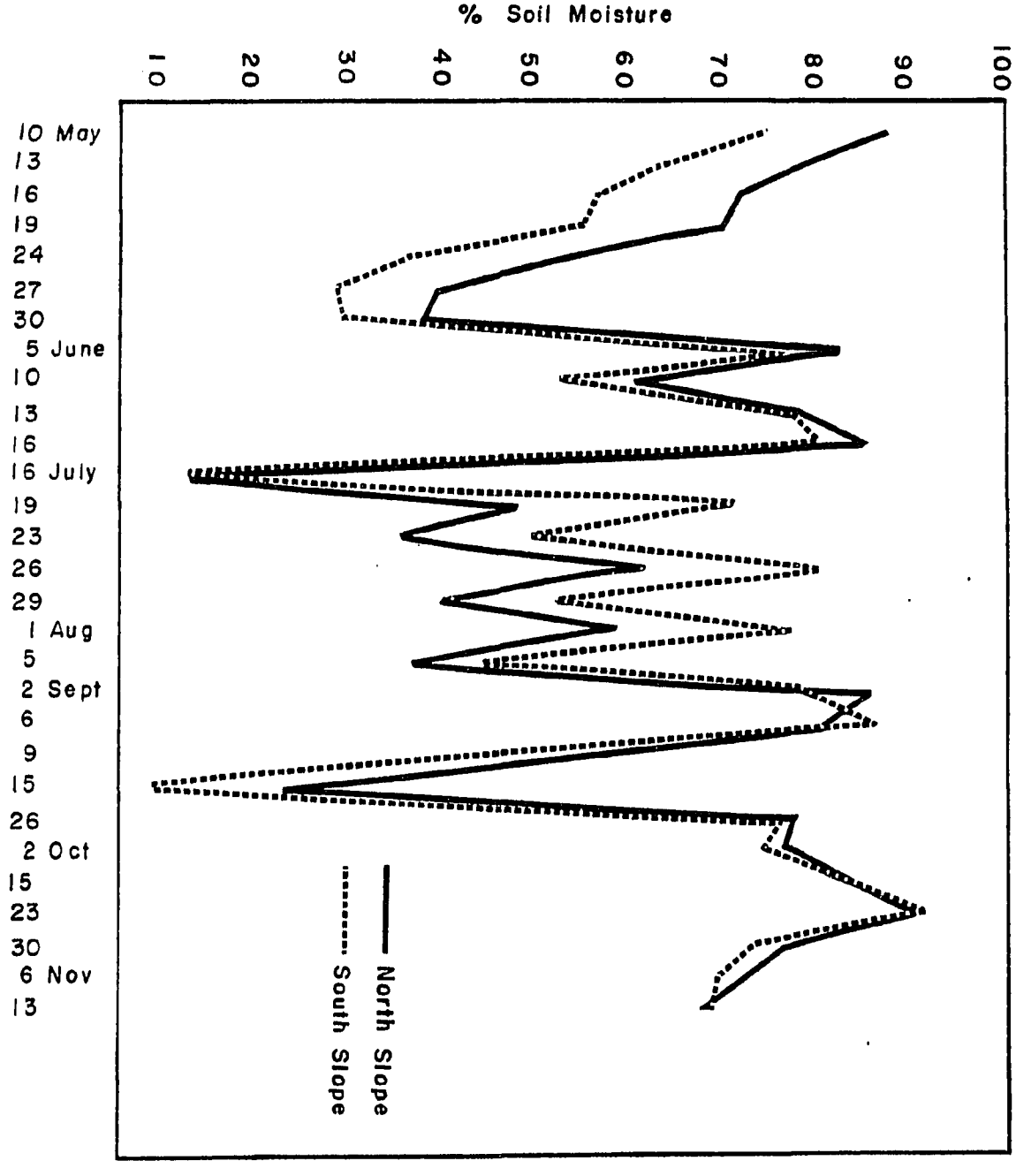
highest rate of evaporation was recorded in May on a south exposure just prior to canopy closure. This is also the period of highest temperature maximum on the south slope. Insolation on south exposures has a warming and drying effect exceeding that of the north slopes in the spring.

Soil Moisture

The results from the soil moisture analysis are difficult to interpret. Numerous problems were encountered with the placement of the blocks. The soil composition, amount of litter and duff, depth of placement relative to the surface of the litter, and the compaction of the soil are all variables which influence readings. Additionally, blocks were frequently disturbed by rodents and deer and in several instances were even devoured by deer.

No large differences between aspects were detected in this study (Figure 9). In the presence of full canopy the difference between soil moisture ranges for north and south aspects was 0.2%. In the absence of canopy, differences were somewhat greater with the south slope averaging 1.4% less moisture. The trend of the differences is in the direction expected, but the magnitude of differences is much less than expected based on results of previous workers. Reasons for this are unclear. Possibly soil moisture at the depths the blocks were buried (five centimeters) does not

Figure 9. Soil moisture for north- and south-facing slopes based on an average of two soil moisture blocks in two plots on each of two aspects


% Soil Moisture
10
20
30
40
50
60
70
80
90
100
10 May
13
16
19
24
27
30
5 June
10
13
16
16 July
19
23
26
29
1 Aug
5
2 Sept
6
9
15
26
2 Oct
15
23
30
6 Nov
13
North Slope
South Slope

accurately reflect moisture content at greater depths. It is worthy of note that the greatest differences were in the absence of canopy.

It was expected that the soil moisture would be higher throughout the year on the north aspect. By observation this certainly seems to be true in the spring when direct insolation is important. As noted earlier, south slopes are frequently dry and warm while north slopes are still icy and wet. This is supported by the trend shown in Figure 9.

During the summer months relative amounts of direct insolation are less important as a factor in the differences between aspects because of the high angle of incidence on both aspects. Surface temperatures are further moderated because of canopy absorption of incoming radiation. These factors tend to equalize the evaporation potential on both north and south slopes. During summer drought both aspects should dry out equally. This is evident in Figure 9 in the transition from the 30th of May to the 16th of July. By mid July the north slope no longer holds a reservoir of soil moisture. Subsequent precipitation is more easily maintained on flat uplands because of less runoff and a greater development of litter. A much greater cover of litter has been shown to occur on the uplands (90.0%) than on the north slope (59.7%) (Johnson-Groh, 1985). Evaporation of soil moisture would be

retarded by a well developed cover of litter.

In September when the canopy begins to open, insolation again becomes an important factor. The south slopes receive direct radiation, warm up and consequently dry out. The litter does little to protect the soil from drying out when radiation is direct. As is shown in Figure 9, the south slope becomes drier again in the fall.

SUMMARY

In summary the north slopes of Ledges State Park have a more moderated microclimate than that of uplands and south slopes. The monthly maximum temperature before the canopy develops averages 8.4^{o}C cooler on the north slope than on the south slope. These results concur with earlier studies.

Differences between north and south slopes in Peck's (1980) study were larger than measured in this study, possibly because of larger extremes in topography. Woodman Hollow is not as broad as the Ledges canyon and thermometers placed at the bottom of Woodman Hollow would be more moderated than those place mid-slope such as was done at the Ledges. Maximum temperatures were higher in exposed sites at the Ledges before canopy. There was little difference in minimum temperatures between the sites at the Ledges.

It is important to note that the minimum temperatures recorded at Boone are generally lower than those at Ledges due to openness of the Boone reading site. Radiative cooling of the soil at night is likely less at the Ledges because of the vegetation cover, although this was not measured.

Evaporation was lower on the north slope. Kucera (1952) found evaporation rates lower on the north and east aspects. In my study evaporation was up to 40% higher on

the south slope than on the north slope. By comparison Potzger (1939) reported 61% higher evaporation on the south slope.

Soil moisture is higher on the north slope during the times when soil surfaces receive direct radiation (spring and fall). Differences found in this study are much less than those found by Potzger (1939) which were 30.0% higher on the north slope.

The moist, cool microclimate of north slopes at the Ledges State Park correlate with the high cover and species diversity of mosses found there relative to south slopes. Within the north slope microclimate, other factors may be acting on the distributions of mosses, but microclimate is the primary factor.

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SECTION II.

ECOLOGY OF TERRICOLOUS BRYOPHYTES AND LICHENS IN RELATION TO VASCULAR PLANT COMMUNITIES AND MICROCLIMATE IN CENTRAL IOWA FORESTS

INTRODUCTION

Classification of bryophyte communities was the primary goal of many early ecological studies of bryophytes (e.g., Gams, 1932; Cain and Sharp, 1938; Bliss and Linn, 1955). In many instances bryophyte communities were easily circumscribed by the substrate and non-quantitative methods of community description were adequate. Quantitative methods for sampling terricolous communities are now widely employed. This brief review concentrates primarily on North American terricolous studies though a few saxicolous studies and European papers have been included where pertinent.

Higinbotham and Higinbotham (1954) used 50 X 20 cm sample plots to describe five terricolous communities in Mt. Rainier coniferous forests. Similarly, Watson (1960) categorized species of mosses on the basis of environmental variables, and Looman (1964) described five cryptogamic associations in grassland communities of Saskatchewan. Others (Hamilton, 1953; Stotler, 1976) have examined various aspects of bryophyte communities using quantitative sampling techniques.

Recently, ordination methods have been used to examine the distributions of terricolous bryophytes and lichens. Some workers (Yarranton, 1967a; 1967b; 1967c; Coleman and Istock, 1980) have shown methods such as principal

components analysis are useful for bryophytes, but these studies primarily tested the methods and yielded little biological information on the species. Bates (1975) used principal components analysis to show that soil nutrients were an important factor in the distribution of mosses. Lechowicz and Adams (1974) found that principal components analysis was ineffective for identifying determinants of bryophyte distribution, but from the same data found that bryophytes sorted along a gradient of moisture by using Bray-Curtis ordinations. Other studies utilizing ordinations (Lambert and Maycock, 1968; Stringer and Stringer, 1974; Foote, 1966) have also provided information on the distributions of bryophytes and lichens relative to environmental gradients.

Some of the most informative studies have been on bryophyte and lichen distributions along topographic gradients (Alpert and Oechel, 1982; Lee and LaRoi, 1979a; Slack 1977). Lee and LaRoi (1979a) and Slack (1977) looked at distributions of mosses along gradients of elevation and moisture in the Canadian Rockies and Adirondack Mountains respectively. Using gradient analysis they were able to describe quite succinctly the distributions of several dominant mosses. Lee and LaRoi also used indirect polar ordination (Bray-Curtis ordination), but it was based on vascular plants rather than mosses. No studies to my

knowledge have compared direct and indirect methods of ordination based on bryophytes only.

Studies of species diversity along environmental gradients have also been made. Oksanen (1983) found that the precipitation-evaporation ratio was the most important gradient relating to diversity. Lee and LaRoi (1979a, 1979b) found that beta diversity was higher along moisture coenoclines than elevation coenoclines, whereas alpha diversity correlated more to elevation than to moisture. Slack (1977) also noted that diversity was correlated with elevation.

Relationships of bryophyte distributions with the occurrence and distribution of vascular plants has been studied (Looman, 1964; Higinbotham and Higinbotham, 1954; Hamilton, 1953; Slack, 1977; McCune and Antos, 1981; Stringer and Stringer, 1974), but only the most recent of these have quantitatively sampled both bryophytes and vascular plants with comparable sampling procedures. McCune and Antos (1981) compared the diversity of several forest layers and found species richness was greatest in the epiphyte and bryoid layers. Stringer and Stringer (1974) sampled mosses and vascular plants in the same plots and concluded that bryophytes are more sensitive to environmental differences than vascular plants. LaRoi and Stinger (1976) compared mosses of white and black spruce

stands across Canada, and found differences in bryophyte cover as well as growth form in the two tree communities.

The present study was undertaken to compare quantitatively and qualitatively the terricolous bryophyte flora of five deciduous forest communities in central Iowa. The purpose of the study is to elucidate relationships between the bryophyte and vascular components, i.e., whether or not moss distributions correlate more with the microclimate, aspect, microtopography, than with vascular plants.

METHODS

The study was undertaken in Ledges State Park, which comprises 447 hectares (1,117 acres) located in central Iowa along the east side of Des Moines River, T83N, R26W, sections 9, 10, 15, 16, 20, 21, in Boone County. Pease Creek drains into the Des Moines River from the northeast, forming a canyon lined with deep (75m) sandstone cliffs. The Pennsylvanian sandstone ledges, for which the park was named, are the most prominent geological feature of the main canyon. Several other smaller drainages empty into Pease Creek and the Des Moines River, creating a complex of steep ravines and well-drained ridges.

The climate for central Iowa is midcontinental with hot humid summers and cold dry winters. Winter (December through February) average temperature is $-6^{0}C$, with an average daily minimum of $-11^{0}C$. Summer (June through August) average temperature is $22^{0}C$, and the average summer daily maximum is $29^{0}C$. The frost-free growing season averages 151 days, and the total annual precipitation is 848 mm, of which 73% falls as rain from April to September. The prevailing wind is from the northwest in the wianter and south in the summer. Summer weather is characterized by thunderstorms often associated with high winds and occasional hailstorms and tornados (Waite, 1967; Anderson

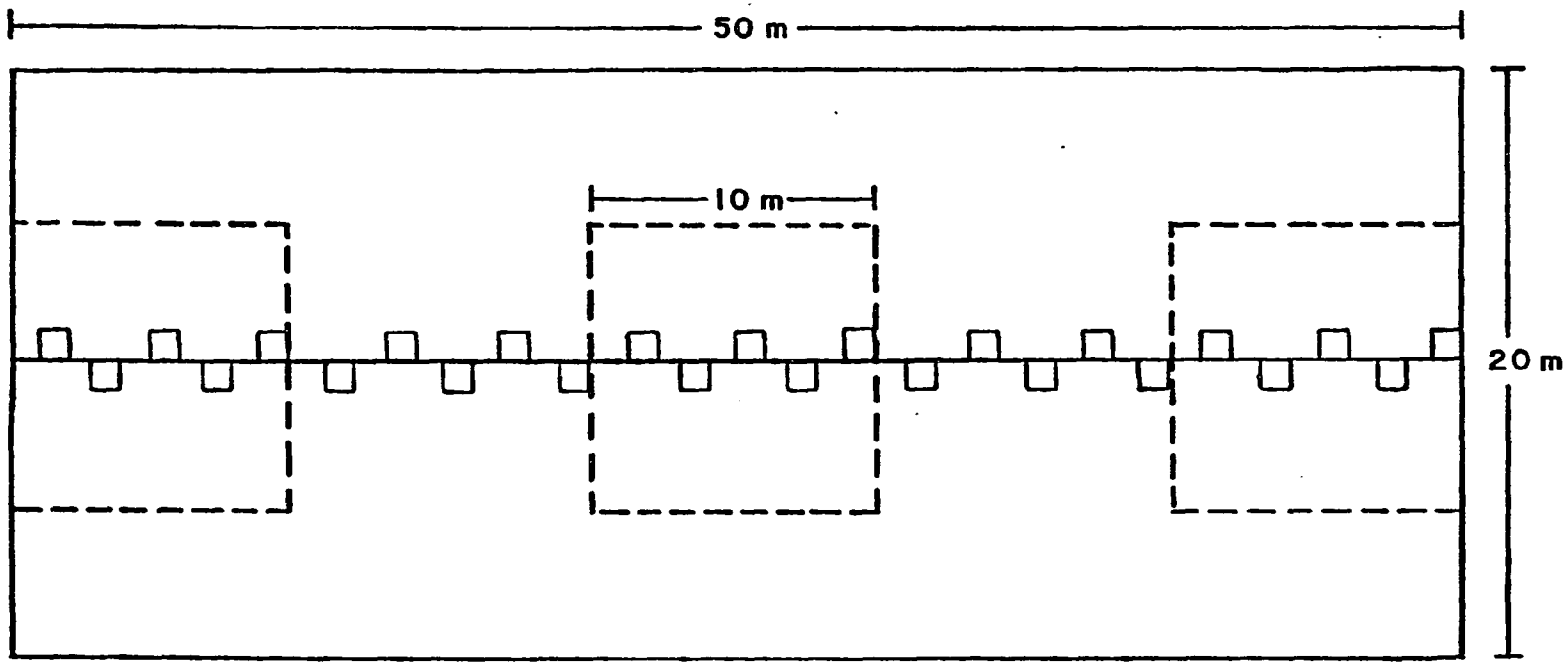
and Dideriksen, 1981).

Five upland vegetation types have been defined for the Ledges (Johnson-Groh, 1985). The deciduous forest of this riverine system is rich for its western location, containing many eastern deciduous species which reach their western limits in the vicinity (Johnson-Groh and Farrar, 1985). Dry upland sites and south-facing slopes are dominated by Quercus alba, while mesic sites are dominated by Tilia americana.

Twenty-three plots were sampled for bryophytes throughout the park. These represent five upland vascular plant vegetation types, and were sampled, ordinated and classified in a previous study (Johnson-Groh, 1983; 1985). Listed from the most xeric to the most mesic and named by the dominant tree species, the vegetation types are: Quercus alba (QA), Quercus alba-Quercus rubra (QAR), Quercus rubra (QR), Quercus rubra-Tilia americana (QRTA), Tilia americana (TA).

In the previous study, permanent 50 X 20 m plots (Figure 1) were established, and the cover of herbs, shrubs and trees were recorded. Each layer of vegetation was ordinated. The plots to be sampled for mosses were chosen from the ordination of communities based on trees. Five plots were sampled in each vegetation type, except in the QRTA type where only three plots were available.

Figure 1. Diagram of a sample plot


50 m
10 m
20 m

In each plot, cover of terricolous mosses was estimated for each species in 25 1 m^2 microplots at alternating meters and sides along the center line (Figure 1). The same method was used to survey the herbaceous layer, allowing direct comparisons between the herbaceous and bryophyte strata.

Mosses which could not be identified confidently in the field were collected and verified using a microscope. The cover of litter and soil was recorded in each microplot. The plots were sampled in August and September of 1984. Binomials for mosses are taken from Crum and Anderson (1981), for liverworts from Schuster (1953), for lichens from Hale (1979), for vascular plants from Gleason and Cronquist (1963).

Direct gradient analysis was used to examine the distributions of bryophytes relative to the aspect. South was the dryest aspect (Section I), and was consequently chosen as the xeric end of the gradient. The north aspect was the most mesic. The plots were positioned along this gradient according to their distance (compass degrees) from south (180^{o}) either in the west or east. No allowance was made for differences between east and west aspects.

Detrended correspondence analysis (DCA) ordinations (Hill, 1979; Hill and Gauch, 1980) were used to reduce the dimensionality of gradients related to species distributions. Alpha diversity was accessed as species

richness, the number of bryophyte species per 50 X 20 meter plot. Spearman rank correlation was used to access similarities in species distributions and richness between the various strata (mosses, trees, herbs) in a particular plot. In this analysis the plots were ranked according to their DCA ordination order from most xeric to most mesic.

Lichens and liverworts as well as mosses were included in this survey. Referral to "bryophytes" or "mosses" hereafter implies inclusion of lichens and liverworts as they occurred.

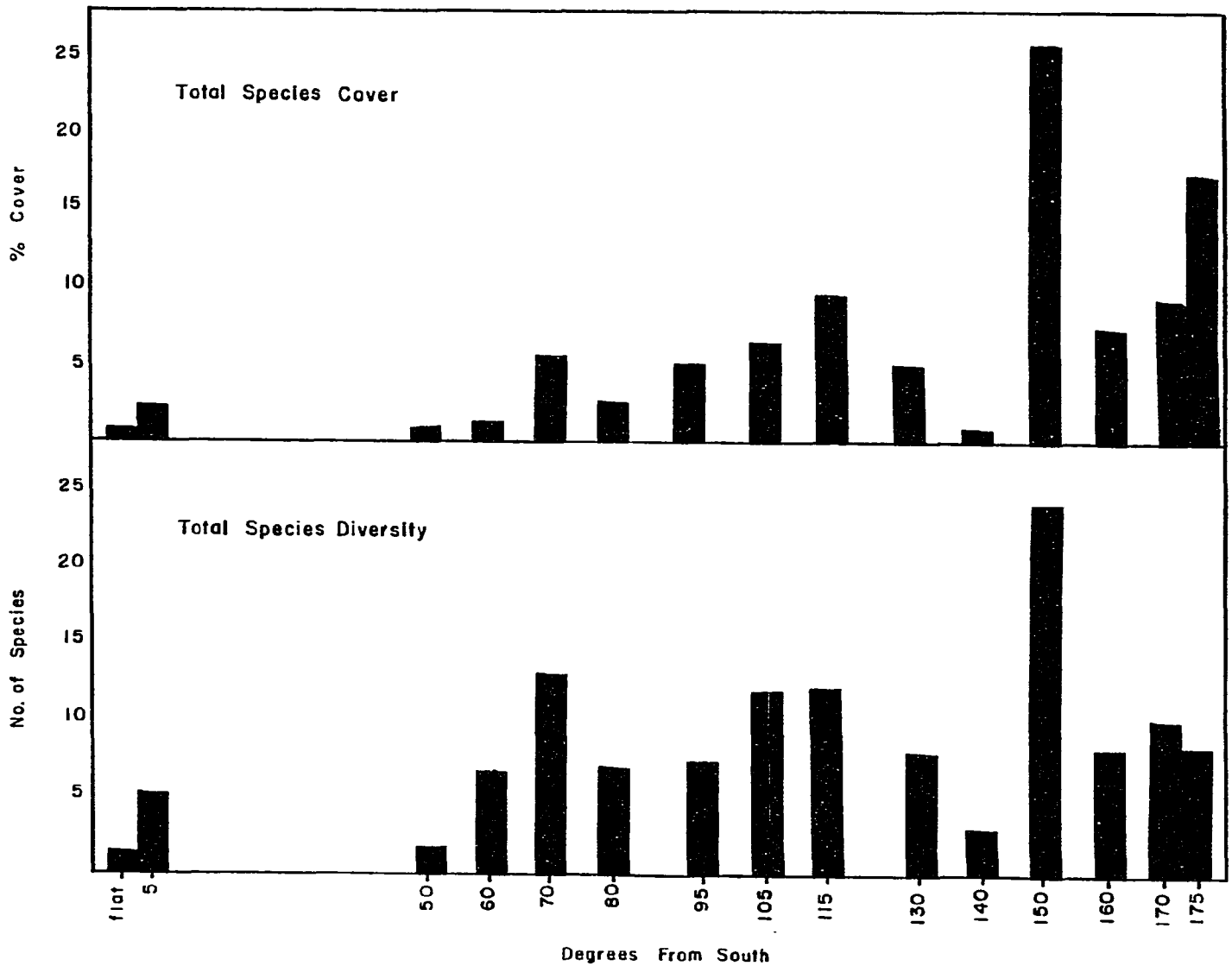
RESULTS

The terricolous bryophyte-lichen flora of the five upland vegetation types was composed of 39 species. Two of these were lichens (Peltigera and Cladonia), three were liverworts (Chiloscyphus, Plagiochilla, and Porella) and the remainder were mosses. Six of the moss species are new to Boone County (Appendix A). The cover and frequency of each moss species by plot is given in Appendix B.

Bryophyte cover in the plots varied from none to 27% with an average of 4.7% cover. Anomodon attenuatus had the highest average cover of all species, ranging up to 9% cover on some sites. Brachythecium oxycladon was the most common moss, found in 16 of the plots. Mnium cuspidatum was also very common occurring in 15 plots.

In direct gradient analysis, stands were ordered along the gradient of aspect (Figure 2), from driest (south-facing) stands to most mesic (north-facing) stands. Total bryophyte cover increases at the north end of the gradient, with a relatively low cover in the south-facing aspects. Total species diversity generally parallels total cover, increasing in the intermediate portions of the gradient and peaking in the northern aspects. However, an increase in total cover at the most mesic site is not accompanied by an increase in diversity, indicating that the high cover of

Figure 2. Direct gradient analysis of species cover and richness. Plots arranged by aspect


Total Species Cover
% Cover
25
20
15
10
5
Total Species Diversity
No. of Species
25
20
15
10
5
flat
5
50
60
70
80
95
105
115
130
140
150
160
170
175
Degrees From South

bryophytes on some north slopes is due to increased abundance of a few mosses rather than to adding different species.

When individual species are projected on the aspect gradient, different distribution patterns become apparent (Figure 3-5). Brachythecium oxycladon has a very high cover on the northern aspects, but is also found, with a moderate cover, throughout the gradient on all aspects. Anomodon attenuatus is very abundant on north aspects, particularly on the northwest aspect, with little or no cover elsewhere. Mnium cuspidatum has highest cover in the intermediate portion of the gradient and slightly less on the northern aspects. Eurynchium hians has a moderate cover on the intermediate and northern portions of the gradient. Rhychostegium serrulatum has highest cover in the intermediate portions of the gradient and also relatively high cover on the south aspects. Fissidens taxifolius has a low, but constant cover throughout the gradient.

Plotted on polar coordinates, east-west as well as north-south aspect preferences are shown (Figures 6). In addition to the patterns discussed above west-facing slope preference of Mnium cuspidatum is apparent.

Detrended correspondence analysis (DCA) produces a two dimensional ordination on which all the plots are clearly separated (Figure 7). (Two plots had no terricolous species

Figure 3. Cover of Brachythecium oxycladon and Anomodon attenuatus plotted on the aspect gradient

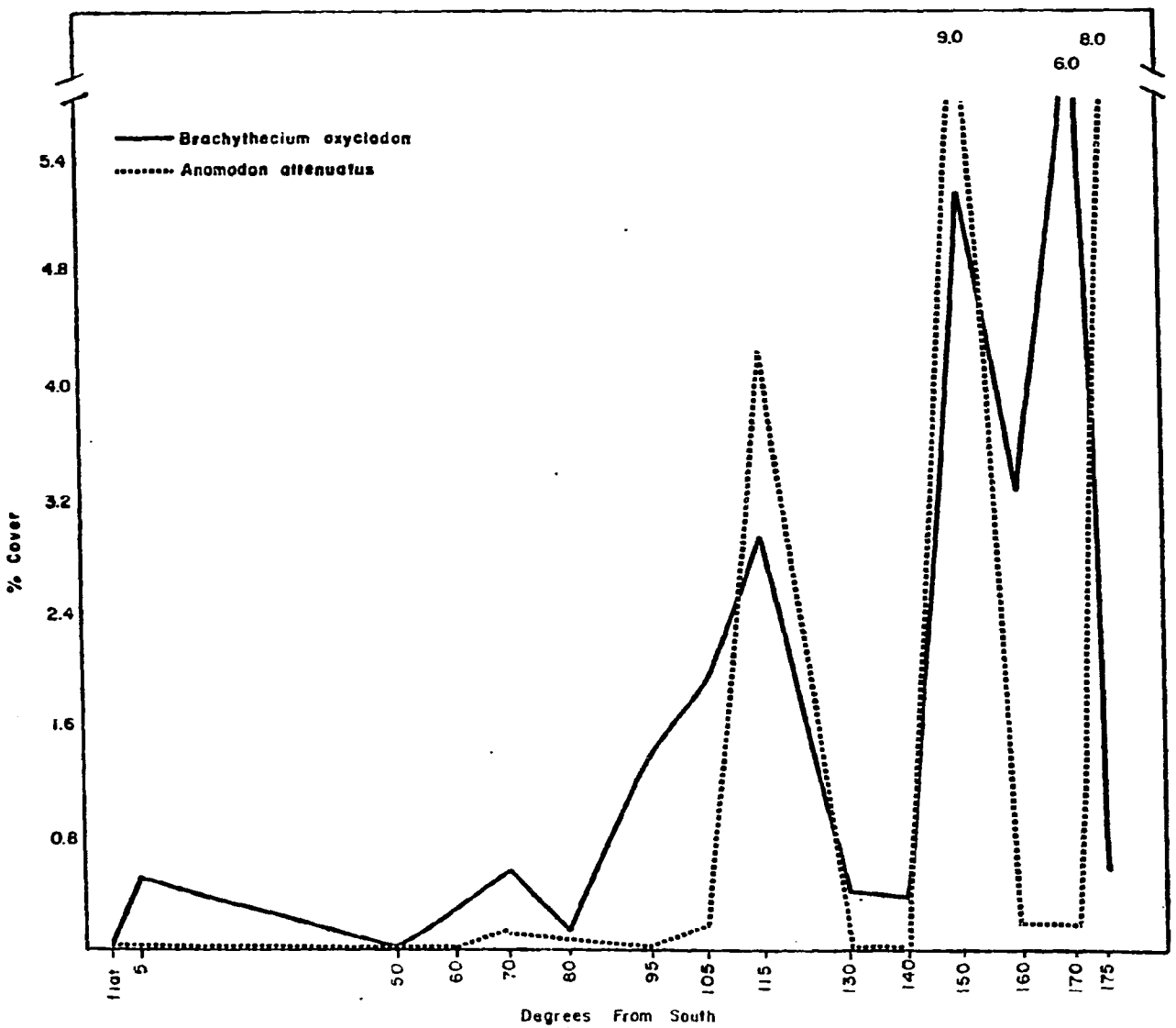

Brachythecium oxycladon
Anomodon attenuatus
% Cover
5.4
4.8
4.0
3.2
2.4
1.6
0.8
9.0
8.0
6.0
flat
5
50
60
70
80
95
105
115
130
140
150
160
170
175
Degrees From South

Figure 4. Cover of Mnium cuspidatum and Eurynchium hians plotted on the aspect gradient

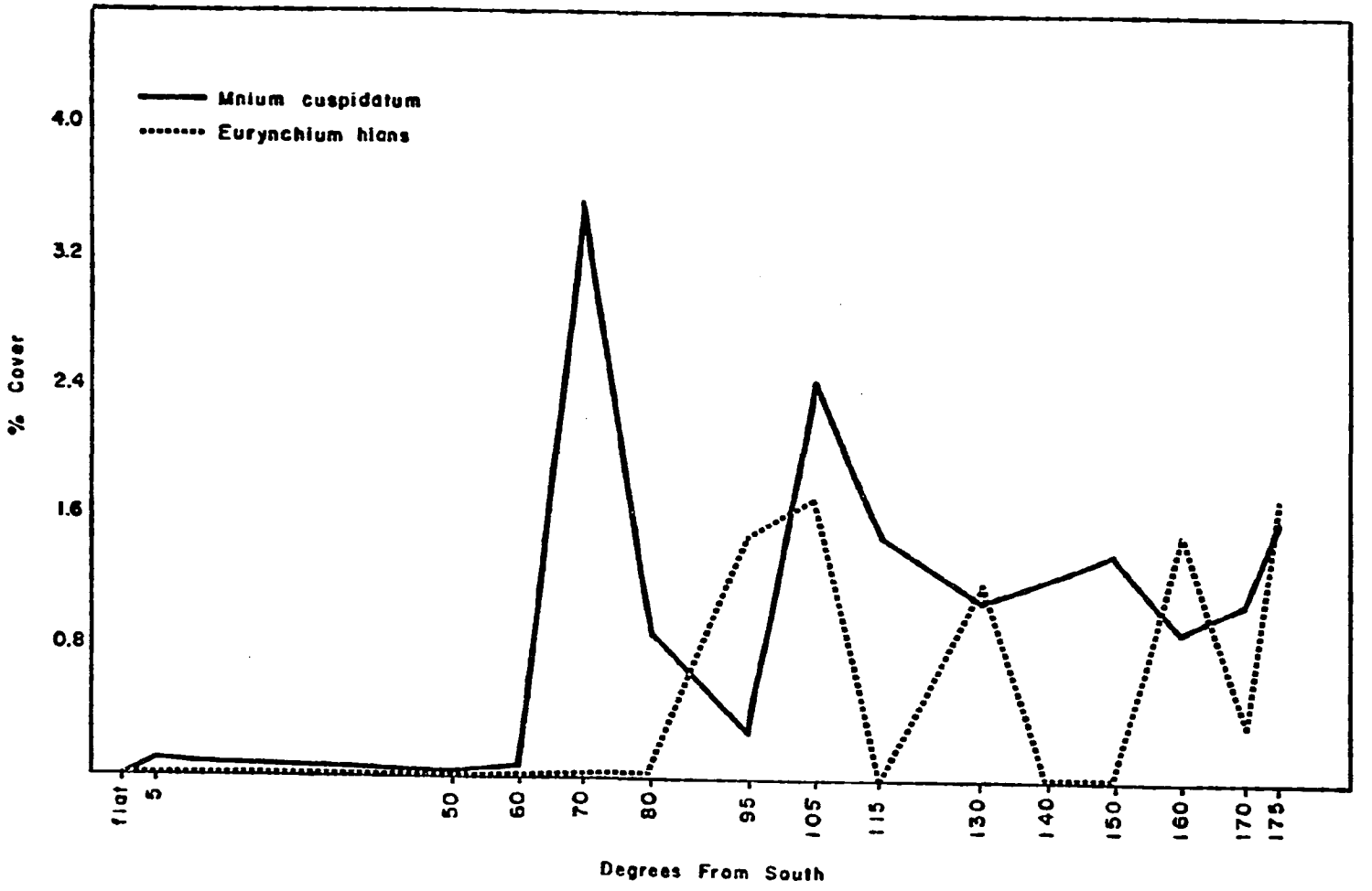

Mnium cuspidatum
Eurynchium hians
4.0
3.2
2.4
1.6
0.8
% Cover
flat
5
50
60
70
80
95
105
115
130
140
150
160
170
175
Degrees From South

Figure 5. Cover of Rhychostegium serrulatum and Fissidens taxifolius on the aspect gradient

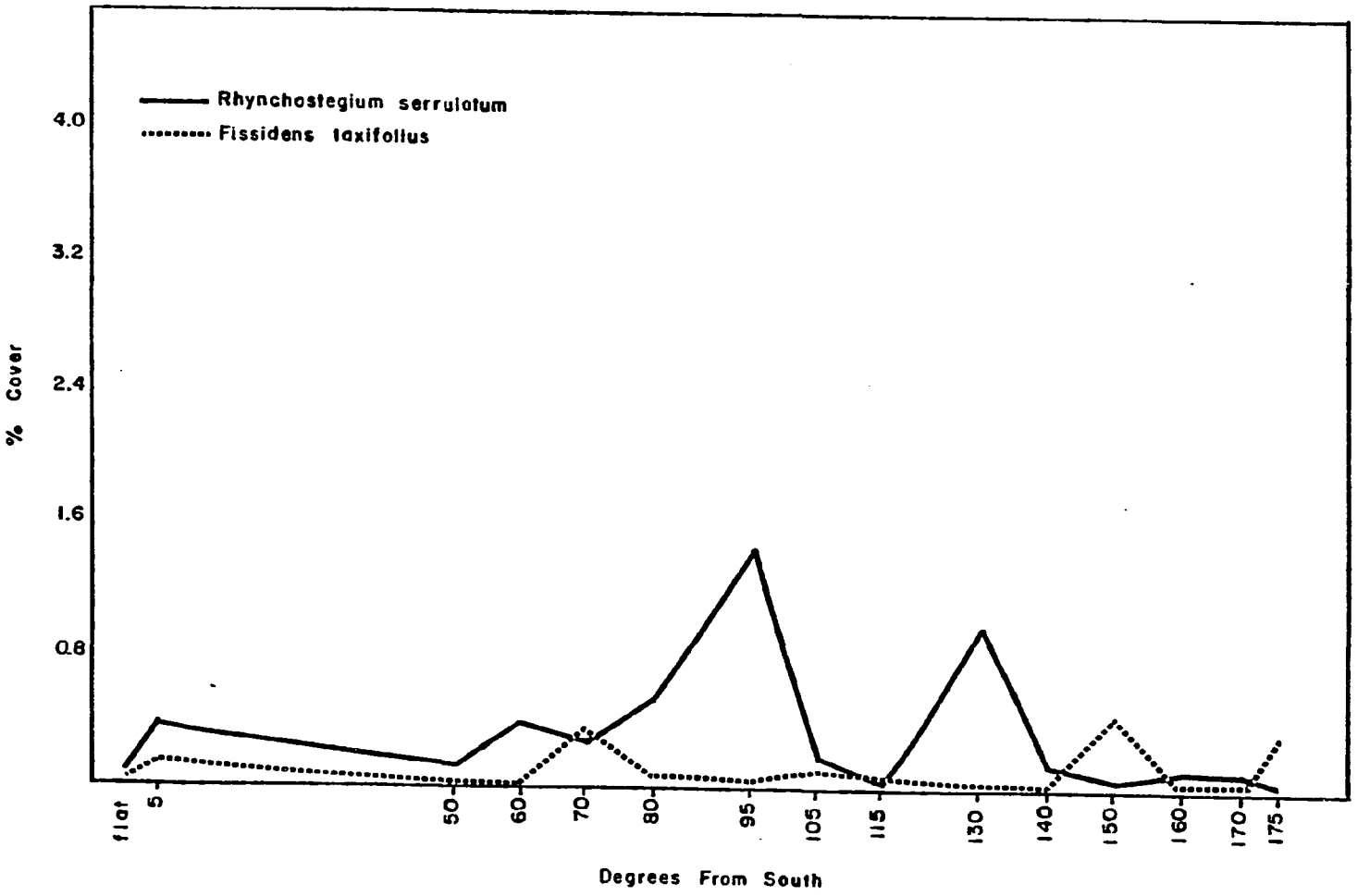

Rhynchostegium serrulatum
Fissidens taxifolius
4.0
3.2
2.4
1.6
0.8
% Cover
flat
5
50
60
70
80
95
105
115
130
140
150
160
170
175
Degrees From South

Figure 6. Cover of common mosses plotted on polar graphs

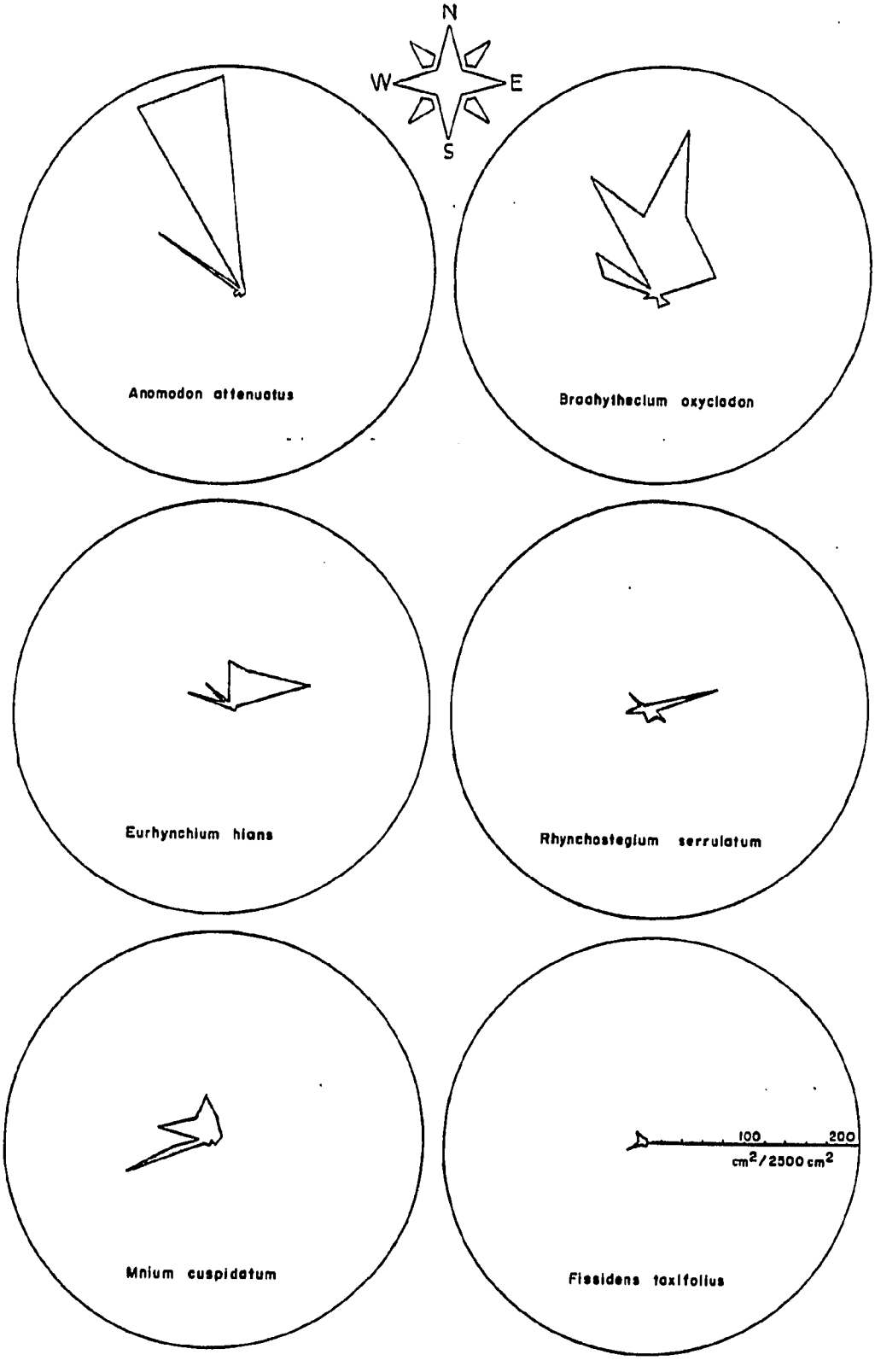
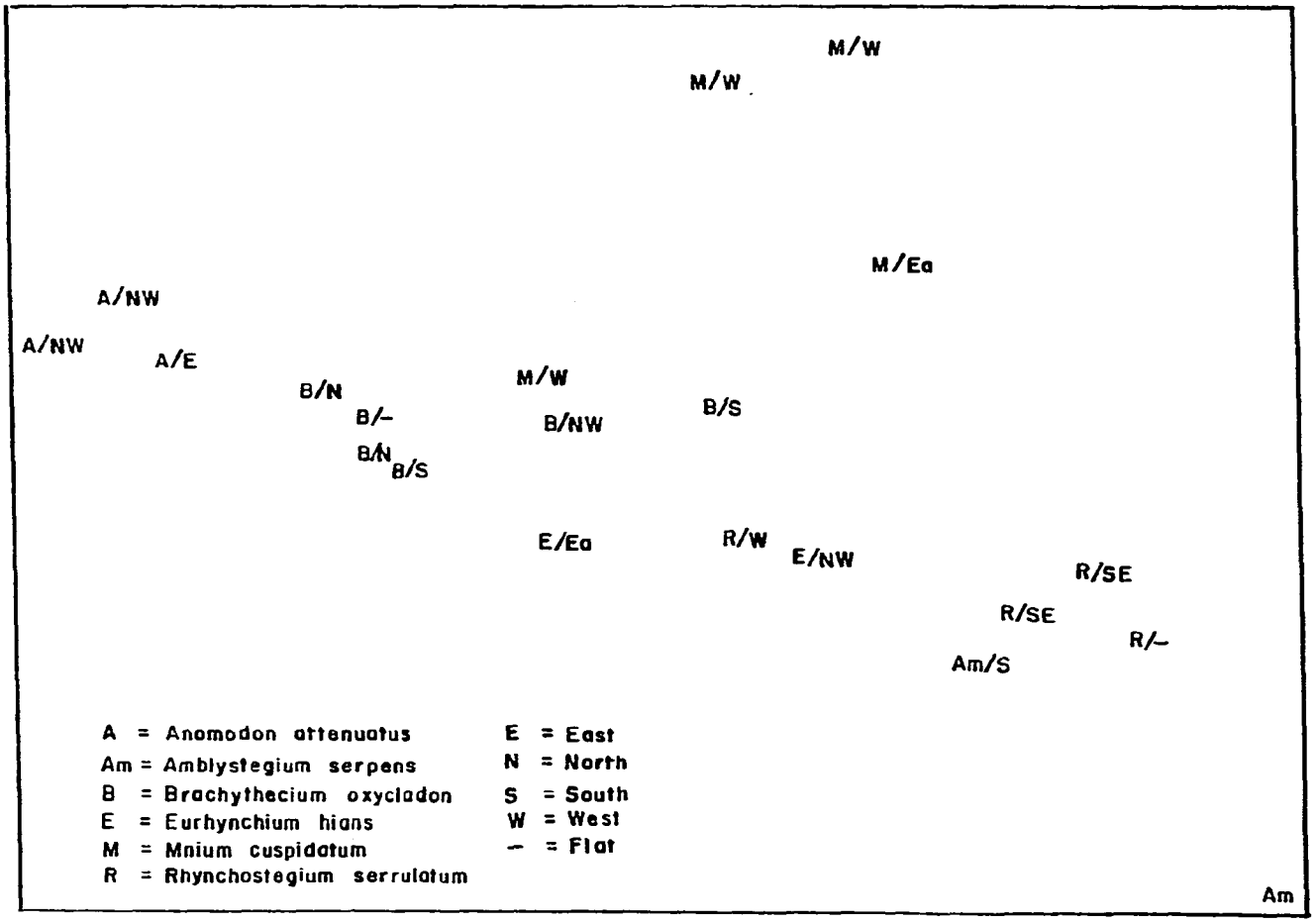

N
W
E
S
Anomodon attenuatus
Brachythecium oxycladon
Eurhynchium hians
Rhynchostegium serrulatum
Mnium cuspidatum
100
200
cm2/2500 cm2
Fissidens taxifolius

Figure 7. DCA ordination of plots based on cover of mosses. Letters indicate dominant moss species and aspect for each plot


M/W
M/W
M/Ea
A/NW
A/NW
A/E
B/N
M/W
B/-
B/NW
B/S
B/N
B/S
E/Ea
R/W
E/NW
R/SE
R/SE
R/-
Am/S
A = Anomodon attenuatus
Am = Amblystegium serpens
B = Brachythecium oxycladon
E = Eurhynchium hians
M = Mnium cuspidatum
R = Rhynchostegium serrulatum
E = East
N = North
S = South
W = West
– = Flat
Am
DECORANA AXIS 2
DECORANA AXIS 1

so were not included in the ordination.) Plots dominated by Anomodon and Brachythecium occur on the left side of the ordination whereas Rhychostegium and Amblystegium dominate plots on the right side. A third axis did not significantly increase the separation of species clustering.

The primary gradient expressed in this indirect ordination is aspect. This is apparent when plot aspects are superimposed on the ordination (Figure 7). North and northwest aspects are found on the left of the ordination with Anomodon and Brachythecium. In the lower right are south and southeast aspects dominated by Amblystegium and Rhychostegium. In the center portion of the gradient are east and west aspects, dominated by Mnium and Eurynchium. Ordinations in which tree density and percent slope were superimposed showed no trends (Figure 8,9).

Relative abundances of selected species are plotted on the ordinations in Figure 10. The aspect preferences are again illustrated. Anomodon attenuatus is largely restricted to wet north and northwest-facing slopes. Brachythecium is common in all but the dryest sites. Eurynchium can be found in the moderately wet sites. Rhychostegium is most common in the moderately dry sites. Mnium is found throughout the areas but has a greater abundance on west and east-facing slopes. Fissidens can be found in all vegetation types in very low cover. It appears

Figure 8. DCA ordination of plots based on cover of mosses with tree density indicated

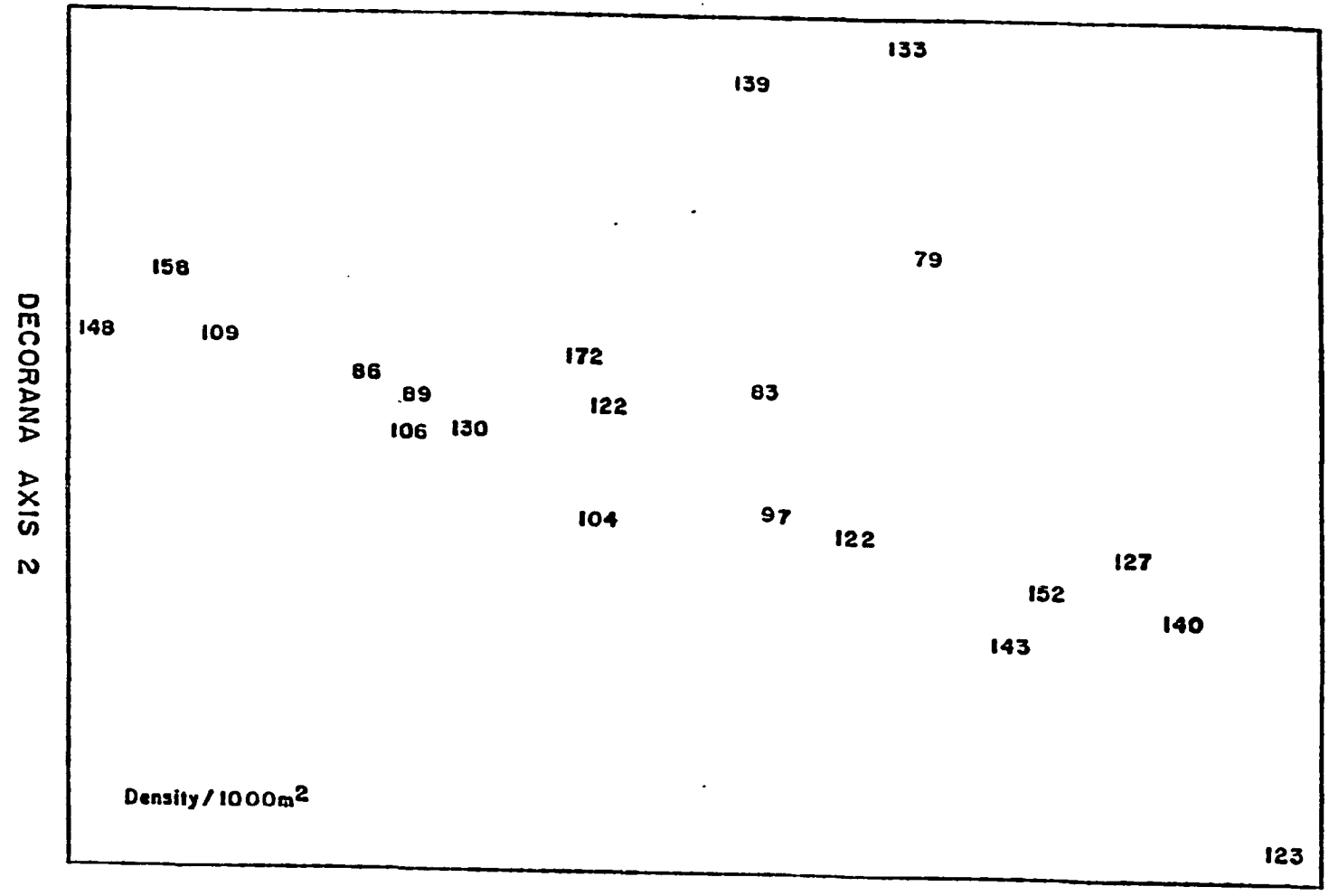

133
139
158
79
148
109
172
86
89
83
122
106
130
104
97
122
127
152
140
143
Density / 1000m2
123
DECORANA AXIS 2
DECORANA AXIS 1

Figure 9. DCA ordination of plots based on cover of mosses with percent slope indicated

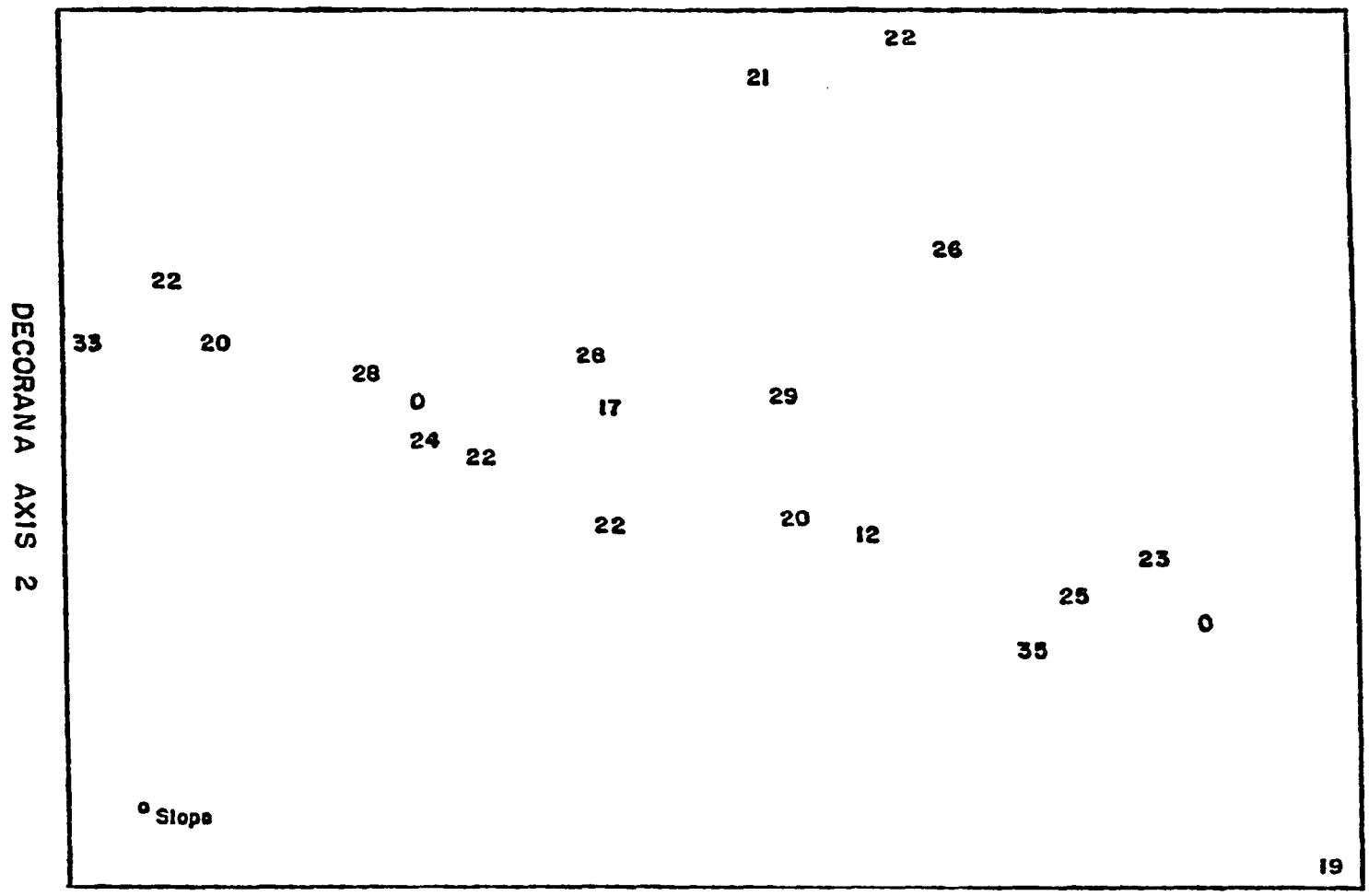
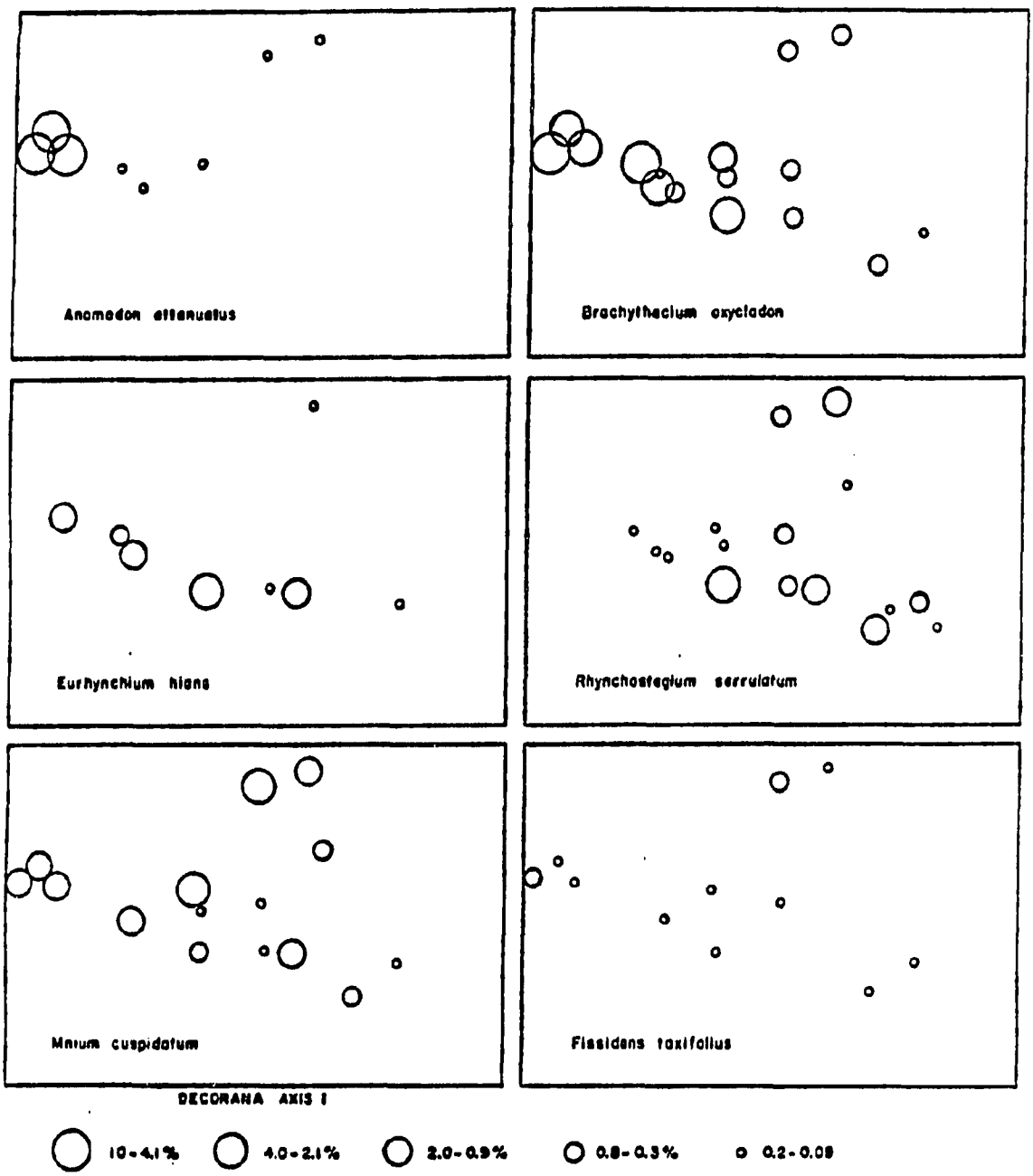

22
21
26
22
33
20
28
28
0
17
29
24
22
22
20
12
23
25
0
35
Slope
19
DECORANA AXIS 2
DECORANA AXIS 1

Figure 10. DCA ordination of plots based on cover of mosses, indicating cover of individual species


Anomodon attenuatus
Brachythecium oxycladon
Eurhynchium hians
Rhynchostegium serrulatum
Mnium cuspidatum
Fissidens taxifolius
DECORANA AXIS I
10-4.1%
4.0-2.1%
2.0-0.9%
0.8-0.3%
0.2-0.08

that these species show habitat divergence along the moisture gradient. No two species have identical habitat preferences, but habitats and thus species may overlap.

The indirect ordination compared favorably with the direct ordination, both indicating aspect as the primary gradient ordering plots. A higher cover and species richness on the moist end (north-facing aspects) of the gradient characterizes both ordinations.

When the dominant tree species are superimposed on the ordination, both low and no correlation between bryophyte and tree distribution patterns can be seen (Figure 11). For example the Quercus alba dominated plot on the left (QA type) is a northwest-facing slope dominated by Anomodon attenuatus. Anomodon attenuatus is commonly found on this aspect, but Quercus alba usually occurs on south slopes. Quercus alba is out of place, it is not a reliable indicator of the bryophyte-level microhabitat. Anomodon is a better indicator of the microclimate as it responds to the microhabitat of the aspect and not to the dominant overstory vegetation.

Spearman rank correlations between mosses, trees, and herbs were based on ordination order of axis one within the separate ordinations. These correlations were moderately high (Table 1), which is interesting because the three ordinations (mosses, trees and herbs) do not represent

Figure 11. DCA ordination based on cover of mosses with dominant tree indicated. Trees in parentheses are common associated species. Trees following a dash are co-dominant species

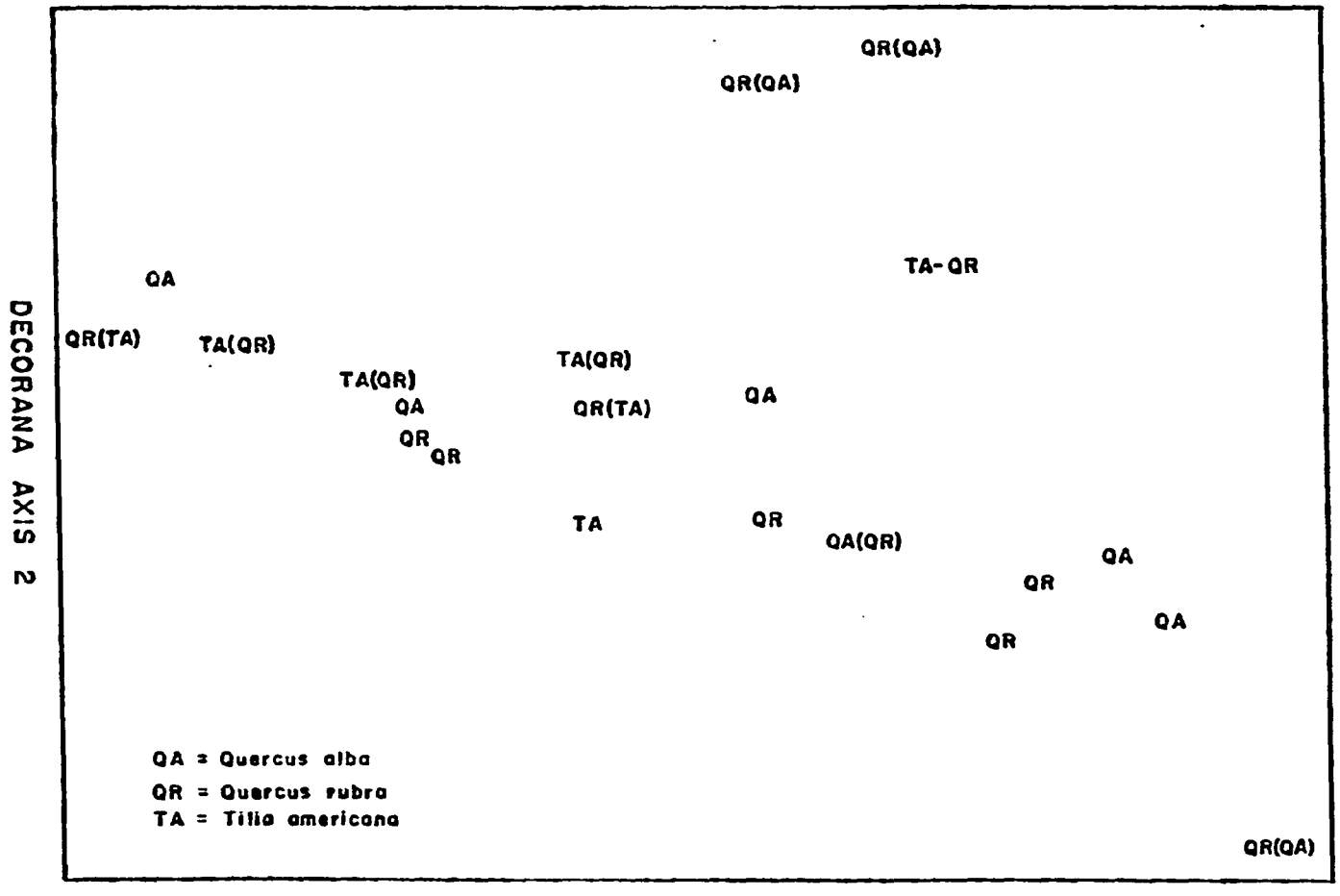

QR(QA)
QR(QA)
QA
TA-QR
QR(TA)
TA(QR)
TA(QR)
TA(QR)
QA
QR(TA)
QA
QR
QR
TA
QR
QA(QR)
QA
QR
QA
QR
QA = Quercus alba
QR = Quercus rubra
TA = Tilia americana
QR(QA)
DECORANA AXIS 2
DECORANA AXIS I

Table 1. Spearman Rank Correlations based on DCA ordination axis 1 order

	Herbs	Trees	Aspect
Mosses	.58*	.42	.62*
Herbs		.52*	.66*
Trees			.57*

*Significant at the .01 level.

precisely the same moisture gradient. The correlation between mosses and herbs is greater than that between mosses and trees. Mosses and herbs had a higher correlation with aspect than did trees.

Distribution of moss species among the vascular plant community types is summarized in Tables 2-4. The most frequently occurring species in the xeric QA type are Brachythecium oxycladon and Rhychostegium serrulatum, with average covers of 0.13% and 0.17% respectively. Eleven species can be found in this type. The most common mosses in the QR type are Anomodon attenuatus, Brachythecium oxycladon, and Rhychostegium serrulatum, and Amblystegium serpens, with 0.88, 0.36, 0.27%, and 0.24% cover, respectively. A total of 18 species can be found in this

Table 2. Average percent cover of bryophytes by vegetation type

	QA	QAR	QR	QRTA	TA
Amblystegium serpens	.03	.002	.24		.05
Amblystegium varium		.03			
Anomodon attenuatus		.03	.88	.04	3.5
Anomodon minor		.01	.005		
Anomodon rostratus	.03	.15	.09		.02
Atrichum undulatum		.23	.03		.01
Aulocomnium heterostichum			.02		
Bartramia pomiformis					.002
Brachythecium acuminatum		.09			
Brachythecium oxycladon	.13	.70	.36	.02	3.9
Bryhnia graminicolor				.08	.66
Bryum caespiticium	.005				
Campylium hispidulum	.04	.003	.06	.004	.1
Chiloscyphus polyanthus					.16
Cladonia sp.		.004			.05
Climacium americanum					.26
Entodon cladorhizans		.02			
Entodon seductrix			.02		
Eurynchium hians	.003	.31		.30	1.38
Fissidens cristatus					1.03
Fissidens taxifolius	.04	.03	.08		.15
Gymnostomum aeruginosum					.001
Leskea gracilescens		.003			.002
Lindbergia brachyptera					.002
Lophocolea minor					.02
Mnium affine		.02			.28
Mnium cuspidatum	.04	.83	.75	.25	1.07
Mnium marginatum					.09
Peltigera canina			.002		.03
Physcomitrium pyriforme	.01	.02	.01		
Plagiochilla asplenoides					.16
Porella platyphylloidea					.06
Rhodobryum roseum					.005
Rhychostegium serrulatum	.17	.48	.27	.07	.59
Taxiphyllum deplanatum		.05	.04		1.25
Timmia megapolitana					.03
Thelia asperella		.01	.01		
Thuidium delicatulum		.07			.08
Weissia controversa	.002	.01	.002		.004

Table 3. Constancy. Proportion of plots in which the species occurs

	QA	QAR	QR	QRTA	TA
Amblystegium serpens	.4	.2	.4		.6
Amblystegium varium		.2			
Anomodon attenuatus		.2	.2	.2	.8
Anomodon minor		.2	.2		
Anomodon rostratus	.2	.4	.4		.6
Atrichum undulatum		.4	.2		.4
Aulocomnium heterostichum			.2		
Bartramia pomiformis					.2
Brachythecium acuminatum		.2			
Brachythecium oxycladon	.6	.6	.6	.4	1.0
Bryhnia graminicolor				.2	.8
Bryum caespiticium	.2				
Campylium hispidulum	.4	.2	.4	.2	.4
Chiloscyphus polyanthus					.2
Cladonia sp.		.2			.2
Climacium americanum					.4
Entodon cladorhizans		.4			
Entodon seductrix			.2		
Eurynchium hians	.2	.6		.2	.8
Fissidens cristatus					.2
Fissidens taxifolius	.4	4	.6		.8
Gymnostomum aeruginosum					.2
Leskea gracilescens	.2		.2		.4
Lindbergia brachyptera					.2
Lophocolea minor					.2
Mnium affine		.2			.6
Mnium cuspidatum	.4	.8	.4	.6	.8
Mnium marginatum					.4
Peltigera canina			.2		.2
Physcomitrium pyriforme	.6	.2	.2		
Plagiochilla asplenoides					.2
Porella platyphylloidea					.2
Rhodobryum roseum					.2
Rhychostegium serrulatum	.6	.8	.6	.6	.6
Taxiphyllum deplanatum		.4	.2		.8
Timmia megapolitana					.4
Thelia asperella		.2	.2		
Thuidium delicatulum		.2			.2
Weissia controversa	.4	.2	.2		.2

Table 4. Relative percent cover of dominant species

	QA	QR	TA
Amblystegium serpens	5	9	3
Anomodon attenuatus		31	25
Brachythecium oxycladon	24	13	28
Bryhnia graminicolor			4
Campylium hispidulum			1
Climacium americanum			2
Eurynchium hians			10
Fissidens taxifolius	8	3	1
Mnium cuspidatum	1	26	8
Physcomitrium pyriforme	3		
Rhychostegium serrulatum	34	9	4
Taxiphyllum deplanatum			9

type. In the TA type, Anomodon attenuatus, Brachythecium oxycladon, Eurynchium hians are most common, with 3.5, 3.9, and 1.4% average cover. There are a total of 30 species in the TA type.

The QAR type has a high abundance of moss species and cover relative to the QA and QR types. The QRTA type has a low cover and diversity relative to the QR and TA types. The latter lack of cover and diversity may be due to the small number of plots sampled. Both of these types could be considered ecotone types and such variation is not unexpected.

Dominant species of the moss flora vary in abundance among the vascular community types, but not in presence-

absence. Species differences among the Ledges terricolous moss communities are more accurately defined by the subdominant species associated with the dominants. Table 5 lists the principal differences between the three main vegetation types. It is the associated and unique species which make the types distinct. Species which are restricted to only one type are more valuable as indicators of that type than are the dominant species. Such species with high fidelity are considered by the Braun-Blanquet school, as the most useful indicators.

Table 5. Bryophyte community characteristics

	QA	QR	TA
Total number of species	11	18	30
Number of unique species	1	2	13
Average % total cover	0.5	2.0	13.8
Average species richness	4.4	6.0	13.0

DISCUSSION

The cover of bryophytes increases from xeric (south aspects) to mesic (north aspects). Bryophytes comprise a significant proportion of the total ground (mosses and herbs) cover (37%) and number of species (26%) on the northern aspects. In other areas bryophytes had less than five percent cover.

Results of this study indicate that the evaporative demand is most important in determining the distribution of bryophytes. Similar results were obtained by Lee and LaRoi (1979a) who found that bryophyte cover increased along a montane moisture gradient. Elevation along the transect was secondarily important. Alpert and Oechel (1982) also found that bryophyte cover correlated with an increase in water availability more than any other factor. Stringer and Stringer (1974) working in southern Manitoba found that vascular plant cover as well as bryophyte cover decreased from mesic to xeric sites.

The high total cover of bryophytes on the more mesic north aspects probably results from the more favorable growing conditions. Cool and moist conditions persist through the summer on north aspects, allowing the mosses to sustain growth for longer periods of time than on drier aspects (see Section I). Furthermore, because north slopes

tend to provide favorable moist areas for longer periods in the summer, bryophyte colonization is more likely. Microdisturbance sites on north slopes may be more favorable for bryophyte colonization because of higher moisture. More frequent desiccation on south slopes may limit rapid growth and colonization by mosses.

Actual cover of bryophytes is difficult to compare among studies utilizing different methods and sites. In almost all other studies, and particularly those by Lee and LaRoi (1979a) and Alpert and Oechel (1982), cover was higher than in this study. It is well documented that bryophytes are an important and major component of montane and arctic ecosystems, and it is expected that total cover values in central Iowa would be less. Slack (1977) found a very low cover of bryophytes in Adirondack deciduous forests as compared to the spruce-fir vegetation at higher elevations. This may in part be due to the more xeric conditions found in eastern deciduous forest as compared to mountane coniferous forests.

Lichens formed only a minor component of the plant community (except as epiphytes) at low elevation in Slack's study (1977), and this is in agreement with the results of the present study, in which only two terricolous lichens were found. Lambert and Maycock (1968) also found fewer lichens in areas of high frequency of deciduous species.

They related this to the lack of substrate, reduction in light intensity at ground level, increased litter, and a more rapid turnover of organic matter.

Since there are no previous studies of terricolous bryophyte distributions in the midwest, direct comparisons are impossible. Because environmental gradients in central Iowa are not as great as those measured by Lee and LaRoi (1979a) and Slack (1977), the differences between species environmental preferences may not be as great. Nevertheless bryophyte species at Ledges show habitat divergence, especially along the moisture gradients, as is seen from the separation of their preference centers. No two species had identical distributions, but their habitats overlap.

Anomodon attenuatus is restricted to fairly moist sites, where it develops a very high cover, higher than any other species in this area. Brachythecium also develops a high cover but in slightly drier sites. Rhychostegium has low cover and only in moderate to dry sites. Some species such as Mnium tend to have their highest cover in the intermediate portions of the gradient. Mnium can be found in the mesic sites with a high cover but tends to be very patchy in distribution. Competitive exclusion or substrate preference may restrict Mnium to these small patches while Anomodon attenuatus has no difficulty establishing itself throughout mesic habitats. Fissidens taxifolius occurs on

slightly disturbed sites and tends to be on vertical exposed sites below an overhang of soil. Slack (1977) also noted the occurrence of Fissidens taxifolius on steep unstable banks.

The total number of bryophyte species per stand ranged from none in two west-facing stands to 26 in a mesic north-facing slope, and averaged 7.8 species. This maximum of species diversity is low compared to that found by Lee and LaRoi in Alberta (1979b) (as many as 33 species). However they studied a much larger gradient and included mosses of all substrates, not just terricolous mosses. Similarly Alpert and Oechel (1982) found a maximum species richness of 34 species in Alaska. Slack found that the maximum species richness in deciduous forest quadrats, in the Adirondack Mountains, was 25, this increased to 30 in spruce-fir quadrats.

Bryophyte species richness shows a positive correlation (.55, $p<.005$) with aspect. Aspect is only an approximation of the moisture gradient. Lee and LaRoi (1979a) found that richness was not correlated with moisture, but rather with elevation. Slack (1977) also found that species richness correlated with elevation ($r=.69$), but neither study compared richness versus moisture at a given elevation.

Moisture availability is the most likely controlling factor of species richness at Ledges. It seems unlikely

that the high species richness (and cover) on the north-facing slopes is due to other factors such as greater microhabitat heterogeneity or micropatterning of the ground surface. There is little difference between areas in this respect except as caused by differences in moisture. Alternatively, litter decomposition is faster and its accumulation less on north slopes, since there is greater moisture, and Tilia americana leaves decompose more readily than Quercus leaves. This may contribute to the high richness and cover on the north slope. However it was shown that north slope mosses such as Anomodon also occur in abundance on north-facing slopes dominated by Quercus alba. It seems unlikely that the litter is the dominant factor controlling species distributions.

Whittaker (1965) postulated that diversity is highest in favorable environments. Other factors being equal (e.g. similar substrate availability), favorable environments for bryophytes are those with frequent wetting or low evapotranspiration rate (Dilks and Proctor, 1975; Pitkin, 1975). A most favorable forest floor environment in central Iowa would be the north-facing slope where temperatures are cooler, and consequently there is less evaporation and more water available to the plants.

Slack (1977) found that total cover of bryophytes was not correlated to diversity. Lee and LaRoi (1979a) also

found that cover and richness did not coincide. Diversity and cover are correlated in this study. Cover increases slightly more than diversity in the middle portion of the gradient, but both increase dramatically on the north-facing aspects. This would be expected since the gradient in this study is much smaller than in Slack's or Lee and LaRoi's study. Slack (1977) did note that within a "vegetation zone" diversity and cover correlated.

Correlation between bryophyte vegetation and vascular plant vegetation at Ledges is evident. The species distributions of moss habitats tend to overlap to a greater extent than do herbs or tress. Other studies have found similar overlap for mosses (Alpert and Oechel, 1982,; Lee and LaRoi, 1979a; Looman, 1964). Alpert and Oechel (1982) stated "In general, it appears that on a scale of kilometers cryptogam communities often have a broader range than vascular communities, while on a scale of meters they often have a narrower range." Anomodon attenuatus can be found throughout the eastern United States, but in any given habitat, it will only be found in specific microsites which are suitable. LaRoi and Stringer (1976) found classifications based on vascular species interfaced well with those based on bryophytes, and meaningful classifications of boreal coniferous forests could be based on the bryophyte component.

Contrary to the results of LaRoi and Stringer (1976), most workers have found that a single system of vegetation zones will generally fail to accurately describe both the bryophytes and vascular plant distributions. Both bryophytes and vascular plants respond similarly to the overall environment. Species with strong affinities for moist conditions will be found in the same vicinity. Generally however the bryophytes are more sensitive to microenvironmental variations. Stringer and Stringer (1974) found that marked divisions between bryophyte communities were not visible where only the vascular composition was considered. Similarly Lambert and Maycock (1968) concluded that lichens were not good indicators of the vascular community, since they occupy microhabitats different from that of vascular plants, not influenced by the overall environment.

The mosses in this study were not classified into communities, as wholly distinct units were not found. Where change did occur between moss assemblages, the vascular plants partially reflected the change. The herbaceous community, because of its size, is influenced more by microclimate than are trees. It would be expected that mosses and herbs would be more closely correlated, because of their mutual susceptibility to microclimate, than would be mosses and trees. Correlations of 0.58 between mosses

and herbs and of 0.42 between mosses and trees provide evidence for this.

In general the distribution of mosses more closely reflects the influence of aspect on the microclimate than do trees. This is expected, as mosses are subjected to similar microclimate while trees are more exposed to the macroclimate and are able to tap deeper reserves of water and nutrients. Influences of aspect are moderated at high levels above the ground and the trees are not subjected to the large differences in microclimate caused by aspect. Therefore mosses can be used to predict microclimate more accurately than they can be used to predict the tree community.

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SECTION III.

ECOLOGY OF CORTICOLOUS BRYOPHYTES AND LICHENS IN RELATION TO VASCULAR PLANT COMMUNITIES AND MICROCLIMATE IN CENTRAL IOWA FORESTS

INTRODUCTION

The relationship of corticolous (bark-dwelling) bryophytes and lichens to the phorophyte (host) species and to the surrounding vascular plant vegetation and microclimate is one that has intrigued and baffled bryophyte ecologists for many years. The primary challenge has been to separate the influence of the host species from all other environmental factors.

Epiphytes have been shown to respond to many factors, including bark characteristics, tree age, height on the tree, exposure, habitat in relation to local environment and geography. It is not possible to treat individual environmental factors in isolation, as the composition and structure of epiphyte communities results from the interaction of all these factors. Host preference and the surrounding microenvironment will be examined here as two of the principal factors influencing epiphyte distribution.

Most workers have concluded that some degree of host specificity or host preference exists for bryophyte and lichen epiphytes. Specificity, as generally used, implies positive association of a particular epiphyte with a particular phorophyte, with the understanding that this association is not exclusive and may change in different geographic regions. Host specificity and host preference

are used interchangeably by most workers, as will be done here.

Numerous studies have been done on bryophyte and lichen epiphytes, including Barkman's monumental work "Phytosociology and ecology of cryptogamic epiphytes" (1958), covering every conceivable aspect of epiphyte ecology. A number of studies have looked at the physical and chemical properties of bark in relation to epiphyte host specificity (Barkman, 1958; Billings and Drew, 1938; Culberson, 1955a; Hale, 1955; Eversman, 1982; Studlar, 1982; Gough, 1975; Jesberger and Sheard, 1973). Barkman reviewed factors such as pH, buffer capacity, salt concentration, tannins, resins, bark relief, flakiness, hardness, water absorption and water retention in regard to their possible affects on bryophyte and lichen growth.

Culberson (1955a) investigated the hardness of bark, which is often credited as one of the factors determining epiphyte distributions. He found no correlation between the bark hardness and epiphyte distributions, except for differences between hardwoods (angiosperms) and softwoods (conifers), which may be due more to bark chemistry and flakiness.

Little quantitative work has been done on the microtopography of the bark, though many authors have noticed the restrictions of some species to rough bark,

knotholes etc. Gough (1975) concluded that exfoliation of bark was the character most important in epiphyte distributions.

Moisture and pH has been looked at in numerous studies (Billings and Drew, 1938; Culberson, 1955a; Barkman, 1958; Jesberger and Sheard, 1973; Gough, 1975; Studlar, 1982; Hale, 1955). Hale (1955) noted that host specificity could be correlated to some extent with bark pH and moisture capacity. The correlation was valid, however, only in small segments of the continuum gradient. Culberson (1955a) ranked phorophytes by their moisture retention, pH and hardness. He noted that there was no apparent relationship between pH and species richness of epiphytes.

Jesberger and Sheard (1973) compared bark pH and scaliness in Saskatchewan and found pH to be the factor most responsible for the separation of crustose and fruticose lichens. The authors conceded the difficulty of deciding if the crustose species on Populus, with its high bark pH, are physiologically adapted to these conditions or are found there because of the suitability of the associated environmental complex.

Except to relate bark pH to species distributions, relatively few workers have attempted to show an actual affect of pH on the growth of epiphytes. The data of Pitkin (1975) indicate that pH affects the growth of epiphyte

species differentially.

The chemical nature of bark has sometimes been given as a possible reason for host specificity of epiphytes. There has been little work in this area other than by Barkman (1958), who divides host trees into three groups based on bark electrolyte content.

Another factor which has been looked at in regard to host specificity includes age of the phorophyte. Age mostly has been correlated with epiphyte succession (Quarterman, 1949; Phillips, 1951; Studlar, 1982). Age has usually been studied by size (measured as diameter). The change in bark with age and the time available for colonization are two critical factors. Slack (1976) has stated that over time competitive interactions among epiphytes may also be important.

The relationship between epiphyte cover and tree size varies between studies. Culberson (1955a) found little increase in the number of epiphyte species with increase in diameter. Slack (1976) found an increase in number of epiphytes on both Fagus grandifolia and Betula alleghaniensis with an increase in diameter, though she found the inverse was true on Acer saccharum (Slack, 1977). Trynoski and Glime (1982) showed a significant increase in percent cover with an increase in diameter for all hosts except Betula. Eversman (1982) found that the percent cover

of lichens decreased as tree size increased, an effect which she attributed to bark sloughing off with increasing age. Beals (1965) found no correlation of lichen cover to the size of the tree or thickness of the bark. Slack (1976) noted that age is not a critical factor for phorophytes whose bark changes insignificantly with time.

It is important to point out here the difficulty of comparing results obtained through different sampling methods. As noted above, Culberson (1955a) found no correlation between diameter and number of species, but he measured only presence and absence of species and not cover. On the other hand, Trynoski and Glime (1982) reported correlation between cover and diameter. It is plausible that cover of a few species may increase with diameter while species richness remains constant. Likewise Hoffman and Kazmierski (1969) point out that cover revealed differences in exposure which presence-absence did not. The northeast side of the tree had a higher cover, but the same number of species as the southwest side.

The height of sampling (vertical distribution) on the tree also affects analysis of epiphyte distributions. Most workers have sampled at discrete levels, most frequently at breast height and at the base (Hale, 1955; Culberson, 1955a; 1955b Beals, 1965; Slack, 1976; Trynoski and Glime, 1982; Rasmussen, 1975). A few have sampled continuously

along transects (Stringer and Stringer, 1974; Hoffman and Kazmierski, 1969). All studies have shown some vertical zonation, with bryophytes most abundant at the base and lichens relatively more abundant with increasing height.

High cover of bryophytes as the tree base has been attributed to the collection of rainfall at the base, protection from desiccating winds, snow cover, and high humidity of surrounding humus-litter. Several physiological studies have shown that bryophytes at the base of the trees are adapted to low light intensity and water logging, whereas those higher on the trunk are adapted to higher light intensity and have a high tolerance to desiccation (Tobiessen et al., 1978; Hosokawa and Kubota, 1957; Hosokawa and Odani, 1957; Hosokawa et al., 1964).

The direction of exposure has been examined by several workers (Trynoski and Glime, 1982; Hoffman and Kazmierski, 1969; Rasmussen, 1975; Hoffman, 1971; Jesberger and Sheard, 1973; Eversman, 1982). In all studies the north or northeast direction had the highest cover of epiphytes.

The affect of macroclimate on host specificity has been compared over wide geographical regions. Culberson's (1955a,b) and Hale's (1955) studies of epiphytes in northern and southern Wisconsin, respectively, still remain as two of the most thorough studies of epiphyte distributions. On Acer saccharum the average number of epiphytes decreased

from seven in the north (Culberson, 1955a) to two in the south (Hale, 1955). They found that many epiphyte species shifted host preference from north to south. Slack (1976) compared epiphytes of the same phorophytes in the Adirondack Mountains and the Blue Ridge Mountains. She found a high similarity of epiphytes on a given phorophyte, within a region, but not between regions. Acer saccharum had the highest similarity of any phorophyte with 52% of the epiphytes in common between both regions. The bryophytes had distinct host preferences within a region.

In most of the preceding studies, epiphytes were shown to have a preference for a particular phorophyte, and in some cases a preference for the direction and height on a phorophyte. While host specificity may account for much of the distribution patterns of epiphytes, few workers would agree that it is the only factor. In fact, host specificity may not be the primary factor in determining epiphyte distributions. The influence of microclimate may override whatever host specificity exists.

Other studies have recorded the affect of local climatic and microclimatic variables on the distributions of epiphytes. Barkman (1958) stated, but did not measure, that surrounding vegetation exerts its greatest influence by affecting humidity. McCune and Antos (1982) found that stand age and moisture gradients affect epiphytes. Hoffman

and Kazmierski (1969) found the epiphytic communities of Pseudotsuga menziesii to vary with respect to site (xeric to mesic) in the Olympic Peninsula. Several sites were compared which differed considerably in rainfall (62 cm to 342 cm annually).

Potzger (1939) measured evaporation on trees in Indiana and found that the highest water loss was on the tree trunk well above the base. He noted higher rates of evaporation in upland areas than in ravines and attributed this to stronger air currents in the former.

Stringer and Stringer (1974) looked at epiphytes over a small area in Manitoba. Along with Hale (1955), they found that the microenvironment was secondarily important to bark characteristics for lichen distributions. For bryophytes, however Stringer and Stringer found microenvironmental factors, especially shade and humidity, of "paramount importance" in determining the overall distribution of epiphytic bryophytes. Phillips (1951) also concluded that the tree species was not the most important factor, except possibly in xeric habitats where some bryophyte species may show a preference for a particular tree species. Beals (1965) found that lichen communities have a marked preference for host species, but that there is considerable overlap of their environmental tolerance, and host specificity was only partially developed for most species.

While these studies are informative for the most part, they have not actually tested the relative importance of microenvironment versus host specificity in a local area. They have inferred that the microenvironment is important, but have generally made comparisons between different phorophytes.

Palmer (1986) addressed questions of host versus microclimate in posing the question "do mosses see the forest or the trees?" He sampled epiphytes of seven tree species in three very different forest types. However, of the seven tree species sampled in this study, only two were present in more than one of the forest types. All other trees were sampled in only one type. Ordination of the trees based on importance values for bryophytes clearly separated four hardwood species from two pine species, with birch in an intermediate position. He concluded that bryophyte species in different areas segregate along the same gradient of bark chemistry and moisture even if the tree species is not the same. Given the great differences in the forest communities sampled (upland hardwood forest and a pine dominated forest), one would expect to see differences in distributions due to both the 'forest environment' as well as to host preference. Because the study failed to compare the same tree species in the different 'forest environments', one can conclude that he

demonstrated neither a strong case for host preference (mosses responding to the trees) or for the effect of microclimate (mosses responding to the forest). It seems pertinent then, to ask the question again under a carefully designed sampling scheme which allows the variables to be held constant.

This study is an attempt to examine the structure and composition of epiphytes in a small macroclimatically uniform region, and to identify environmental factors which influence the community composition. Epiphyte communities of the same phorophytes are compared in different topographic sites and different vascular plant communities. In this manner the variable of bark (host preference) can be held constant and the effect of the microenvironment assessed. Host preference is tested by sampling different phorophyte species within the same topographic site and vascular plant community, thus holding microclimate constant, with the exception of the influence of phorophyte bark.

METHODS

The study was conducted at Ledges State Park, which comprises 447 hectares (1,117 acres) located in central Iowa along the east side of Des Moines River, T83N, R26W, sections 9, 10, 15, 16, 20, 21, in Boone County. Pease Creek drains into the Des Moines River from the northeast, forming a deep (75m) canyon lined with sandstone cliffs. The Pennsylvanian sandstone ledges, for which the park was named, are the most prominent geological feature of the main canyon. Several other smaller drainages empty into Pease Creek and the Des Moines River, creating a complex of steep ravines and well-drained ridges.

The climate for central Iowa is midcontinental, with hot humid summers and cold dry winters. Winter (December through February) average temperature is $-6^{0}C$, with an average daily minimum of $-11^{0}C$. Summer (June through August) average temperature is $22^{0}C$, and the average summer daily maximum is $29^{0}C$. The frost-free growing season averages 151 days, and the total annual precipitation is 848 mm, of which 73% falls as rain from April to September. The prevailing wind is from the northwest. Summer weather is characterized by thunderstorms often associated with high winds and occasional hailstorms and tornados (Waite, 1967; Anderson and Dideriksen, 1981).

The vascular plant vegetation of Ledges State Park has been documented, and five upland vegetation types were defined in a previous study (Johnson-Groh, 1985). The deciduous forest of this riverine system is rich for its western location, containing many eastern deciduous species which reach their western limits in the vicinity (Johnson-Groh and Farrar, 1985). Dry upland sites and south-facing slopes are dominated by Quercus alba, while mesic sites are dominated by Tilia americana.

Fifteen plots to be sampled for bryophytes were sampled throughout the park. These represent three upland vascular plant vegetation types, and were ordinated and classified in a previous study (Johnson-Groh, 1983; 1985). Listed from the most xeric to the most mesic and named by the dominant tree species, the vegetation types are: Quercus alba (QA), Quercus rubra (QR), Tilia americana (TA).

In the vascular vegetation study, permanent plots 50 X 20 meters were established, and the cover of herbs, shrubs and trees were recorded, as described in Johnson-Groh (1983; 1985). Each layer of vegetation was ordinated separately. The plots to be sampled for mosses were chosen from the ordination of communities based on trees, and represent the three vegetation types listed above. Five plots were sampled in each vegetation type.

In each plot five individuals of five tree species were

sampled. To insure inclusion in a documented vegetation type no trees outside the plot were selected. The tree species sampled were: Acer nigrum, Ostrya virginiana, Quercus alba, Quercus rubra, and Tilia americana.

The trees were selected using five random coordinates within the plot. At each point the nearest stem of the five species was sampled. In clumps of the same species, the stem nearest the random point was sampled. Only trees with a diameter at breast height (dbh) greater than 15 cm were sampled for epiphytes, except for Ostrya, for which a minimum dbh of 10 cm was used. A total of 236 trees were sampled.

Four sides of each tree (north, east, south, and west) were sampled for epiphytes. At each direction a tape was positioned from the base of the tree, extending up to a height of one meter. Cover of epiphytes was recorded along the tape. Each time the tape intercepted an epiphyte the length of intercept was recorded. This was done for the length of the tape in intervals of 10 cm, resulting in ten categories of cover.

Trees which were forked were considered separate stems if the division occurred below 0.5 meter. In forked stems where the fork interfered with tape placement on the appropriate direction, the tape was placed on the other stem in the appropriate direction. This stem then was eliminated

from further tree sampling. Dead trees were included only if they had died relatively recently and the bark was completely intact.

The dbh and the diameter at ground height (dgh) were recorded for each tree. The direction and degree of lean of the tree was recorded. Trees which were forked were noted, including the number of forks.

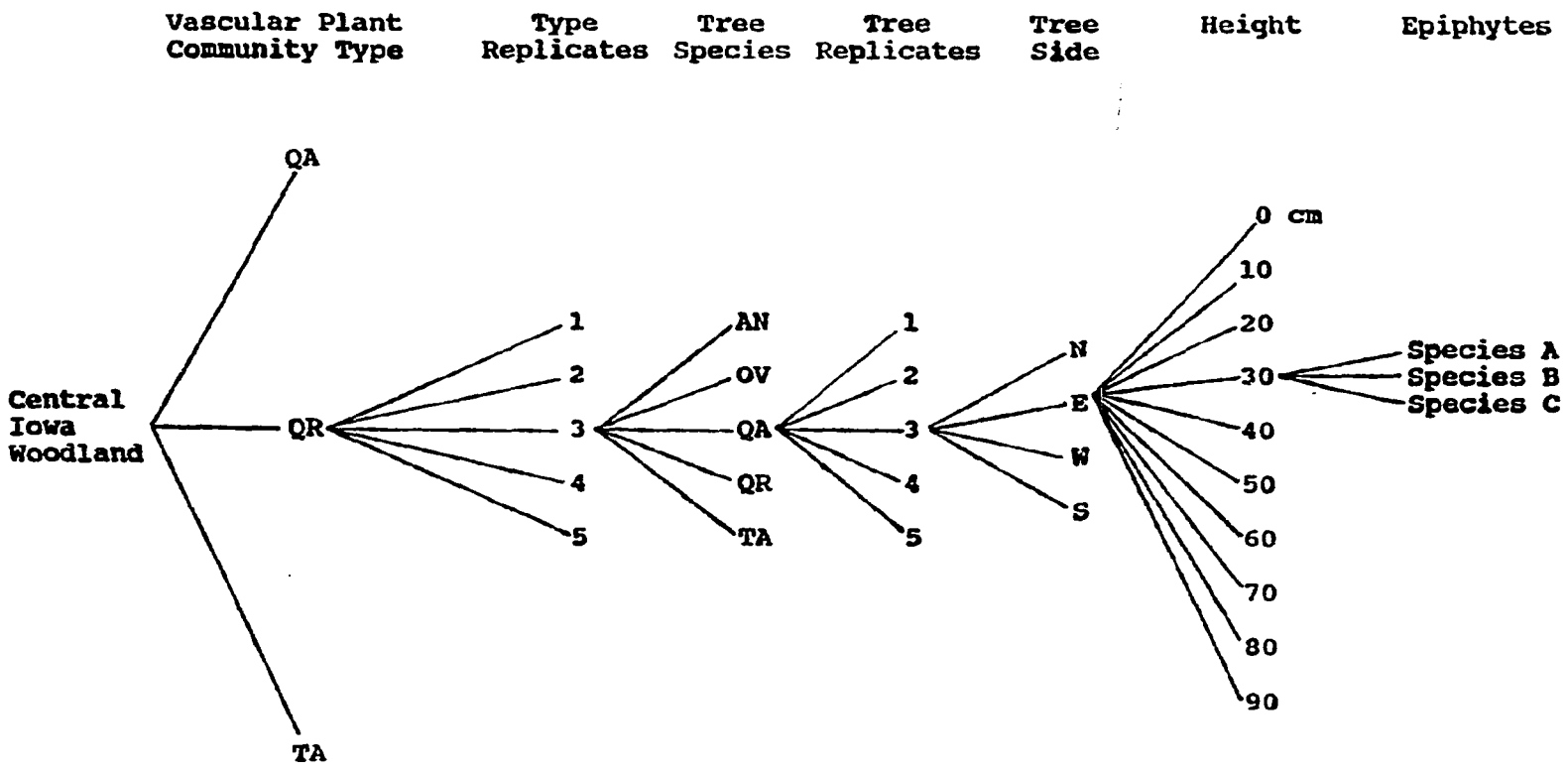
Through this sampling design (Figure 1), comparisons of the vegetation type, tree species, height, direction, tree size, and moss species can be made. Only the relationships between the vegetation type, tree species, and moss species will be discussed here.

This method proved to be a fast and easy way of surveying epiphytes, providing information on height and direction as well as actual cover estimates. Unlike other methods, the plot size is consistent for all trees regardless of the dbh. Cylindrical quadrats as used by Hale (1955), Culberson (1955a) and several other workers, vary in area with the tree size, so this increase in area sampled must be considered when comparing trees of different size. Likewise the methods of McCune and Antos (1982), recording mosses as hits when intercepted every 2.5 cm along a tape at breast height, is size dependent.

The use of a line-intercept allows estimates of cover to be made quickly. This was more accurate and precise than

Figure 1. Stucture of sampling scheme

Data Structure



contiguous quadrats. Problems of quadrat placement on tree trunks with very fluted and contorted bases were eliminated.

It should be noted that the tree base was sampled up to one meter and no higher because of sparsity of epiphyte cover at higher levels. Epiphytes in central Iowa, except for a very few species, are restricted to the lower portions of the tree trunk. Little additional information was to be gained by sampling up to 1.4 m (breast height), as other workers have done. Except for a few studies in which contiguous quadrats were used, most previous studies have confined sampling to a quadrat at breast height and occasionally one at the base or halfway between.

Mosses which could not be identified confidently in the field were collected for later verification with a microscope. The plots were sampled in June through September of 1986. Binomials for mosses are taken from Crum and Anderson (1981), for liverworts from Schuster (1953), and for lichens from Hale (1979), and Hale and Culberson (1970).

Direct gradient analysis was used to examine the distributions of bryophytes relative to the aspect gradient. South was the dryest aspect (see Section I) and consequently was chosen as the xeric end of the gradient. The north aspect was the most mesic. The plots were positioned along this gradient according to their distance (compass degrees)

from south (180°), either in the west or east. No allowance was made for differences between east or west aspects.

Detrended correspondence analysis (DCA) ordinations (Hill, 1979; Hill and Gauch, 1980) were used to reduce the dimensionality of variables related to species distributions. Alpha diversity was measured as species richness, i.e., the number of bryophytes per tree or 50 X 20 meter plot.

In this survey only common and abundant lichens were recorded. The number of lichens encountered does not represent the entire corticolous lichen flora of Iowa. Bryophytes (mosses and liverworts) were the principal target of this study. However, as lichens co-occur and possibly compete with bryophytes, the lichens must be included, at least in a general way, to allow for interpretation of bryophyte distributions. Unless noted otherwise, referral to "bryophytes" or "mosses" hereafter implies inclusion of lichens and liverworts as they occurred.

RESULTS

The corticolous bryophyte-lichen flora of the three upland vegetation sites studied was composed of 30 species. Five of these were lichens (Candelaria, Graphis, Lepraria, Parmelia, Physcia), three were liverworts (Frullania spp., Porella) and the remainder were mosses. Four mosses and two liverworts are new to Boone County (Appendix A). A summary of the cover on all trees is given in Appendix D.

Epiphyte cover on the five tree species varied from none to 276 cm cover (out of a possible 400 cm/tree), with an average of 78.6 cm/tree. Table 1 lists the moss species and their total cover over all trees sampled (236 trees), as well as their relative cover. Anomodon attenuatus, Anomodon minor, Frullania eboracensis, Leskea gracilescens, Lepraria membranacea and Physcia orbicularis account for 80% of the epiphyte cover in central Iowa. A summary of the diameter, cover, species richness, and number of trees sampled in each plot is given in Table 2.

Table 3 lists the average cover of epiphytes by tree species and vegetation type. Quercus rubra supported the highest cover (119.6 cm/tree) of the five trees sampled, and Acer nigrum (70.2 cm/tree) had the lowest (excluding Ostrya virginiana which is in a much smaller size class). The TA vegetation type had the highest cover (108.0 cm/tree) of the

Table 1. Total and relative cover for all species

Species	Cover	Rel. Cover
Amblystegium serpens	142.4	0.01
Anomodon attenuatus	2887.8	0.15
Anomodon minor	3743.5	0.20
Anomodon rostratus	502.0	0.03
Brachythecium acuminatum	609.0	0.03
Bryhnia graminicolor	12.2	0.0007
Campylium hispidulum	8.8	0.0005
Candelaria concolor	53.8	0.003
Climacium americanum	6.0	0.0003
Entodon compressus	667.6	0.04
Entodon seductrix	327.6	0.02
Eurhychium hians	3.2	0.0002
Fissidens cristatus	11.2	0.0006
Fissidens subbasilaris	1.0	0.00005
Frullania eboracensis	1108.5	0.06
Frullania inflata	170.6	0.01
Graphis scripta	388.8	0.02
Lepraria membranacea	1189.0	0.06
Leskea gracilescens	4491.0	0.24
Lindbergia brachyptera	8.8	0.0005
Mnium cuspidatum	139.8	0.01
Orthotrichum pumilum	20.6	0.001
Parmelia bolliana	32.4	0.002
Physcia orbicularis	1671.8	0.09
Platygyrium repens	186.0	0.01
Porella platyphylla	10.6	0.0005
Pylaisiella selwynii	8.2	0.0004
Taxiphyllum deplanatum	74.4	0.004
Thelia asprella	161.8	0.01
Tortella humilis	0.2	0.00001

Table 2. Dbh, cover, richness and number of trees sampled per plot (ave./tree ± std. error)

Plot No.	n	DBH	Cover	Richness
QA TYPES				
1	15	23.8 ± 3.0	70.8 ± 14.8	4.3 ± 0.4
7	10	16.4 ± 3.2	24.0 ± 13.5	2.1 ± 0.4
25	10	22.2 ± 5.4	41.0 ± 11.5	3.1 ± 0.3
31	14	31.5 ± 5.3	107.9 ± 22.3	4.5 ± 0.7
45	11	26.3 ± 5.4	65.6 ± 16.4	2.5 ± 0.4
QR TYPES				
2	21	19.3 ± 2.0	44.5 ± 8.7	3.5 ± 0.4
4	15	24.3 ± 3.2	40.2 ± 5.6	3.0 ± 0.2
9	16	20.7 ± 3.7	40.8 ± 14.8	3.6 ± 0.3
14	18	24.0 ± 3.0	108.5 ± 14.9	4.6 ± 0.4
26	16	28.9 ± 3.8	45.7 ± 12.1	3.5 ± 0.4
TA TYPES				
3	18	28.6 ± 3.9	38.1 ± 7.1	5.0 ± 0.4
12	21	30.6 ± 4.2	105.2 ± 15.7	5.9 ± 0.5
24	19	25.5 ± 2.7	163.1 ± 13.9	7.1 ± 0.4
41	16	27.8 ± 3.7	142.6 ± 17.9	6.9 ± 0.6
50	16	24.8 ± 4.3	90.9 ± 12.1	4.3 ± 0.4

Table 3. Average cover of mosses and lichens (top line) and for mosses only (bottom line) (ave./tree ± std error)

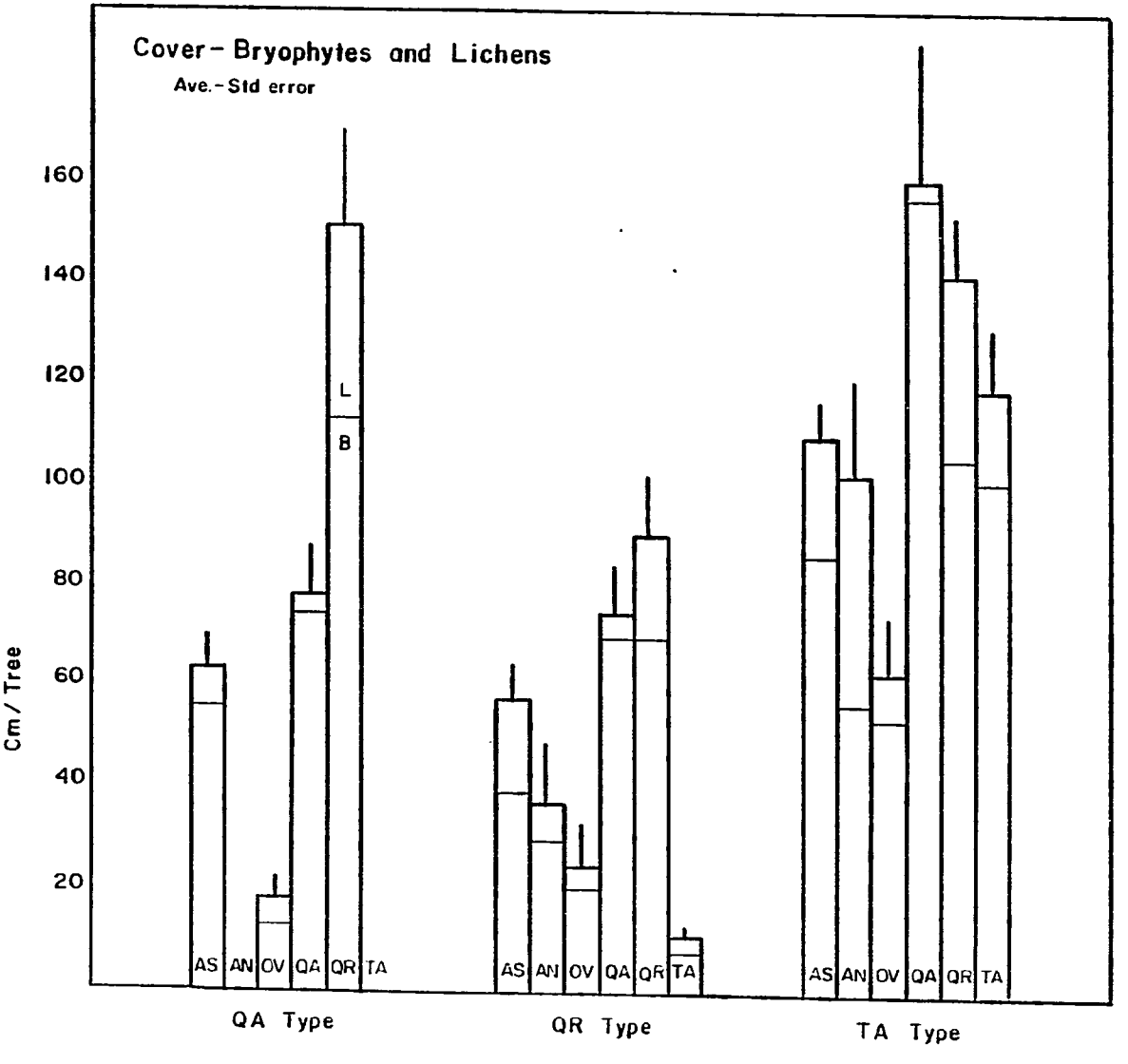
	All Types	QA Type	QR type	TA type
All	78.6 ± 4.4	64.7 ± 8.3	56.7 ± 5.9	108.0 ± 7.6
Species	64.5 ± 3.8	56.4 ± 7.1	48.3 ± 5.0	85.4 ± 6.8
AN	70.2 ± 13.0		38.4 ± 14.4	102.0 ± 18.1
	43.5 ± 9.6		29.4 ± 12.3	57.6 ± 14.0
OV	36.2 ± 5.5	19.9 ± 4.0	24.2 ± 7.0	62.9 ± 12.5
	30.4 ± 5.5	13.4 ± 3.6	22.2 ± 7.0	54.7 ± 12.8
QA	83.2 ± 7.2	78.1 ± 9.7	74.7 ± 8.1	159.1 ± 37.1
	80.8 ± 7.1	76.5 ± 9.4	70.9 ± 7.8	159.0 ± 37.1
QR	119.6 ± 9.3	149.4 ± 23.7	88.9 ± 13.1	139.8 ± 13.3
	91.5 ± 6.8	113.4 ± 17.4	70.3 ± 9.8	105.1 ± 9.6
TA	101.0 ± 14.3		10.4 ± 2.5	119.1 ± 14.7
	85.0 ± 12.7		7.0 ± 3.6	100.5 ± 13.1

communities, followed by QA type (64.7 cm/tree) and QR type (56.7 cm/tree). These numbers decrease consistently, but only slightly over tree species and types if the cover of lichens is eliminated.

Cover was highest in the TA type for all species except QR (Figure 2). Ostrya had almost twice as much cover in the TA type as in the QA type. Quercus rubra supported slightly greater cover in the QA type. Lowest average cover was in the QR type for all trees except Ostrya. No trees of Acer nigrum and Tilia americana occurred in the QA type.

Figure 2. Cover of bryophytes and lichens by tree species in different vegetation types. Cover of lichens is represented above the dividing line, moss cover is represented below the line

AS = All Species
AN = *Acer nigrum*
OV = *Ostrya virginiana*
QA = *Quercus alba*
QR = *Quercus rubra*
TA = *Tilia americana*


Cover - Bryophytes and Lichens
Ave. - Std error
Cm / Tree
160
140
120
100
80
60
40
20
L
B
AS AN OV QA QR TA
AS AN OV QA QR TA
AS AN OV QA QR TA
QA Type
QR Type
TA Type

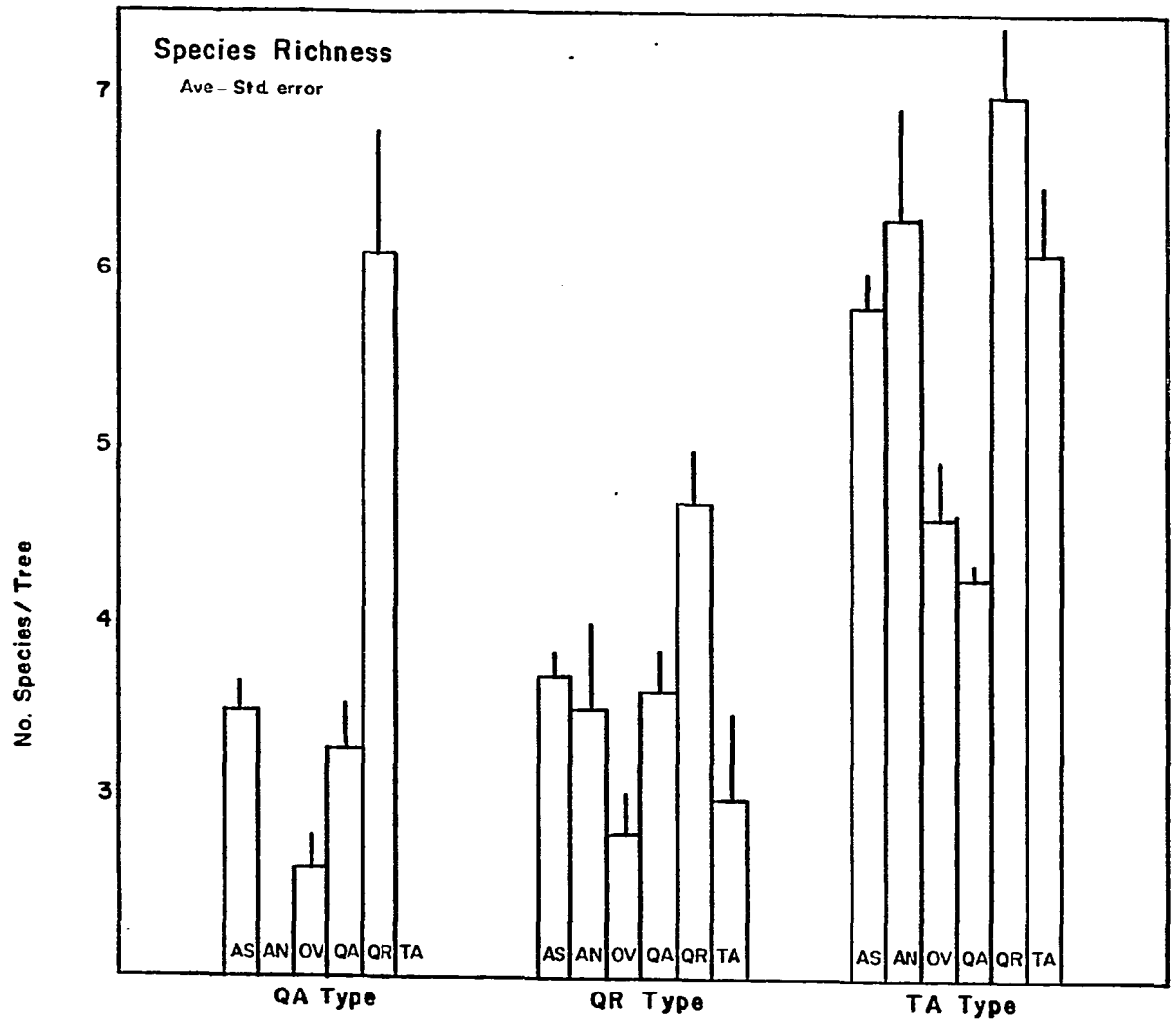
Species richness was generally highest on Quercus rubra (5.8) and lowest on Quercus alba (excluding Ostrya) (Table 4). The TA type had the highest species richness (5.8) followed by QR type (3.7) and QA type (3.5). If the lichens are eliminated from this analysis the same trends are evident, with Quercus rubra and the TA type having the highest species richness. Species richness was highest in the TA type for all tree species (Figure 3).

Table 4. Average species richness for mosses and lichens (top line) and for mosses only (bottom line)(ave./tree ± std error)

	All Types	QA Type	QR type	TA type
All	4.4 ± 0.1	3.5 ± 0.2	3.7 ± 0.2	5.8 ± 0.2
Species	3.3 ± 0.1	2.5 ± 0.1	2.8 ± 0.1	4.2 ± 0.2
AN	4.9 ± 0.5		3.5 ± 0.5	6.3 ± 0.7
	3.1 ± 0.4		2.4 ± 0.4	3.8 ± 0.6
OV	3.3 ± 0.2	2.6 ± 0.2	2.8 ± 0.3	4.6 ± 0.4
	2.3 ± 0.2	1.5 ± 0.1	2.1 ± 0.2	3.4 ± 0.3
QA	3.5 ± 0.2	3.3 ± 0.3	3.6 ± 0.3	4.3 ± 1.1
	3.0 ± 0.2	2.8 ± 0.2	3.0 ± 0.2	4.0 ± 0.9
QR	5.8 ± 0.3	6.1 ± 0.7	4.7 ± 0.3	7.0 ± 0.4
	4.3 ± 0.2	4.4 ± 0.6	3.6 ± 0.3	5.0 ± 0.3
TA	5.6 ± 0.4		3.0 ± 0.5	6.1 ± 0.4
	4.1 ± 0.3		2.4 ± 0.5	4.5 ± 0.3

Figure 3. Species richness of bryophytes and lichens by tree species in different vegetation types

AS = All Species
AN = *Acer nigrum*
OV = *Ostrya virginiana*
QA = *Quercus alba*
QR = *Quercus rubra*
TA = *Tilia americana*


Species Richness
Ave - Std. error
No. Species / Tree
7
6
5
4
3
AS AN OV QA QR TA
QA Type
AS AN OV QA QR TA
QR Type
AS AN OV QA QR TA
TA Type

The influence of the host (bark) on moss distribution is important. Quercus rubra consistently (except for QA in the TA type) has the highest cover and richness in all types. The bark of Q. rubra is the roughest of all trees sampled and provides a variety of microsites for bryophyte growth. The other species have smooth (Tilia, Acer) or somewhat flaky plate-like bark (Q. alba, Ostrya), and generally have a lower cover and richness when compared in the same vegetation type.

Table 5 gives the cover of epiphyte species on the five host species. Tables 6-8 compare epiphytes on host species in the three vegetation type. Host preferences are evident for most epiphyte species. When considered over all types Anomodon attenuatus has its highest cover on T. americana. In the QR type it prefers Q. alba over other species and is in fact absent from the few T. americana trees present in that type. Anomodon minor strongly prefers Q. alba over all types with no exceptions. Frullania eboracensis is highest on Q. rubra over all types except in the TA type, where it has a slightly higher cover on Acer nigrum. Lepraria membranacea has its highest cover on Q. rubra with no exceptions. Leskea gracilescens has its highest cover on Q. rubra when averaged over all types, and only slightly higher on Tilia in the TA type. Likewise Physcia orbicularis has its highest cover on Q. rubra when averaged over all types,

Table 5. Cover of epiphyte species by trees over all types (cm/tree)

Species	AN	OV	QA	QR	TA
Amblystegium serpens	2.0	0.2	1.5	0.1	0.1
Anomodon attenuatus	7.6	3.7	12.4	16.3	28.8
Anomodon minor	11.8	10.9	27.4	10.8	22.1
Anomodon rostratus	1.7	2.2	2.5	2.0	2.1
Brachythecium acuminatum	0.7	0.2	6.6	3.4	1.7
Bryhnia graminicolor		0.2			
Campylium hispidulum			0.2	0.1	0.1
Candelaria concolor	0.4	0.2	0.1	0.5	0.1
Climacium americanum				0.1	
Entodon compressus	0.5	0.1	3.4	7.8	0.8
Entodon seductrix			1.1	4.8	
Eurhychium hians	0.1				0.1
Fissidens cristatus		0.2		0.1	
Fissidens subbasilaris			0.1		
Frullania eboracensis	8.6	2.0	0.3	10.0	4.8
Frullania inflata	1.1	0.4		1.8	0.4
Graphis scripta	12.4	0.1	0.1	0.3	1.5
Lepraria membranacea	1.8	0.1	2.0	12.4	10.6
Leskea gracilescens	8.6	10.1	25.1	28.8	22.5
Lindbergia brachyptera	0.1			0.1	0.1
Mnium cuspidatum	0.2	0.1	0.4	1.6	0.6
Orthotrichum pumilum	0.1	0.1		0.2	0.1
Parmelia bolliana	0.2	0.1		0.4	0.1
Physcia orbicularis	11.9	5.4	1.0	14.3	4.0
Platygyrium repens	0.2			2.9	0.4
Porella platyphylla					0.4
Pylaisiella selwynii			0.2		
Taxiphyllum deplanatum	0.3	0.1		1.0	0.4
Thelia asprella		1.9	1.0	0.1	
Tortella humilis		0.1			
No. Trees sampled	26	72	50	58	30
Species Richness	20	21	18	24	22

Table 6. Cover of epiphyte species by trees in the QA type (cm/tree)

Species	AN	OV	QA	QR	TA
Amblystegium serpens		0.1	1.1		
Anomodon attenuatus			10.8	1.7	
Anomodon minor			14.6	0.1	
Anomodon rostratus		0.8			
Brachythecium acuminatum			10.6	14.6	
Bryhnia graminicolor					
Campylium hispidulum			0.1		
Candelaria concolor		0.3	0.1	0.1	
Climacium americanum					
Entodon compressus			1.4	3.1	
Entodon seductrix			2.1	27.7	
Eurhychium hians					
Fissidens cristatus					
Fissidens subbasilaris					
Frullania eboracensis		0.8	0.4	15.3	
Frullania inflata					
Graphis scripta				0.4	
Lepraria membranacea			0.9	2.8	
Leskea gracilescens		7.6	33.1	47.4	
Lindbergia brachyptera				0.6	
Mnium cuspidatum		0.1	0.3	2.5	
Orthotrichum pumilum		0.2		0.1	
Parmelia bolliana		0.1		0.2	
Physcia orbicularis		6.2	0.6	32.5	
Platygyrium repens					
Porella platyphylla					
Pylaisiella selwynii					
Taxiphyllum deplanatum					
Thelia asprella		4.0	1.9		
Tortella humilis					
No. of Trees Sampled	0	25	25	10	0
Species Richness	0	10	14	16	0

Table 7. Cover of epiphyte species by trees in the QR type (cm/tree)

Species	AN	OV	QA	QR	TA
Amblystegium serpens	1.8		2.3		
Anomodon attenuatus	3.8		11.8	6.0	
Anomodon minor	7.6	9.2	30.4	14.5	1.0
Anomodon rostratus			0.8	2.2	
Brachythecium acuminatum	0.9	0.4	1.6	1.6	
Bryhnia graminicolor					
Campylium hispidulum			0.4		
Candelaria concolor	0.5	0.1	0.1	1.1	
Climacium americanum					
Entodon compressus	0.9	0.2	6.3	4.0	1.0
Entodon seductrix					
Eurhychium hians					
Fissidens cristatus					
Fissidens subbasilaris					
Frullania eboracensis	3.4	1.3	0.2	5.5	0.2
Frullania inflata	0.2	1.0		3.5	1.2
Graphis scripta	1.6		0.1	0.2	
Lepraria membranacea			3.8	7.3	
Leskea gracilescens	9.7	9.3	19.2	24.9	3.5
Lindbergia brachyptera					
Mnium cuspidatum	0.2	0.2		0.1	
Orthotrichum pumilum	0.1	0.1		0.3	0.1
Parmelia bolliana				0.1	
Physcia orbicularis	7.0	1.8	0.1	10.0	3.4
Platygyrium repens	0.5			3.4	
Porella platyphylla					
Pylaisiella selwynii			0.2		
Taxiphyllum deplanatum	0.1	0.1		0.2	
Thelia asprella		0.4	0.1	0.1	
Tortella humilis					
No. Trees Sampled	13	22	21	25	5
Species Richness	15	12	15	18	7

Table 8. Cover of epiphyte species by trees in the TA type (cm/tree)

Species	AN	OV	QA	QR	TA
Amblystegium serpens	2.3	0.4		0.1	0.1
Anomodon attenuatus	11.3	10.6	25.4	33.8	34.5
Anomodon minor	16.0	23.2	91.6	11.3	26.3
Anomodon rostratus	3.4	5.3	26.6	2.7	2.5
Brachythecium acuminatum	0.5	0.2	7.4	0.6	2.0
Bryhnia graminicolor		0.5			
Campylium hispidulum				0.1	0.1
Candelaria concolor	0.2	0.1		0.1	0.1
Climacium americanum				0.3	
Entodon compressus		0.2		9.8	0.7
Entodon seductrix					
Eurhychium hians	0.1				0.1
Fissidens cristatus		0.4		0.1	
Fissidens subbasilaris			0.2		
Frullania eboracensis	13.8	3.9	0.5	12.5	5.8
Frullania inflata	2.0	0.2		0.6	0.2
Graphis scripta	23.2	0.1		0.4	1.8
Lepraria membranacea	3.6	0.1		22.2	12.6
Leskea gracilescens	7.5	13.3	4.6	24.8	26.3
Lindbergia brachyptera	0.1			0.1	0.1
Mnium cuspidatum	0.3	0.2	2.6	2.9	0.6
Orthotrichum pumilum	0.1	0.1		0.8	0.1
Parmelia bolliana	0.4	0.1		0.8	0.1
Physcia orbicularis	17.0	7.9	0.1	11.2	4.1
Platygyrium repens				3.5	0.4
Porella platyphylla					0.4
Pylaisiella selwynii					
Taxiphyllum deplanatum	0.5			2.2	0.4
Thelia asprella					
Tortella humilis		0.1			
No. Trees Sampled	13	25	4	23	25
Species Richness	18	19	9	22	22

but in the TA type it shows a strong preference for Acer nigrum.

These data show that the species host tree provides an important influence on epiphyte growth, but not a completely dominating influence. Epiphytes may shift preferences in different microenvironmental conditions, as shown by shifting patterns just outlined. Of the epiphytes which occurred on at least three of the five tree species, two had highest cover on Acer, one on Ostrya, four on Q. alba, thirteen on Q. rubra, and one on Tilia.

Most epiphytes exhibited a preference for a host species, but could be found on several species. Only a few species were fairly restricted to one host. For example, Graphis scripta was found in high cover on Acer and Platygyrium repens on Q. rubra.

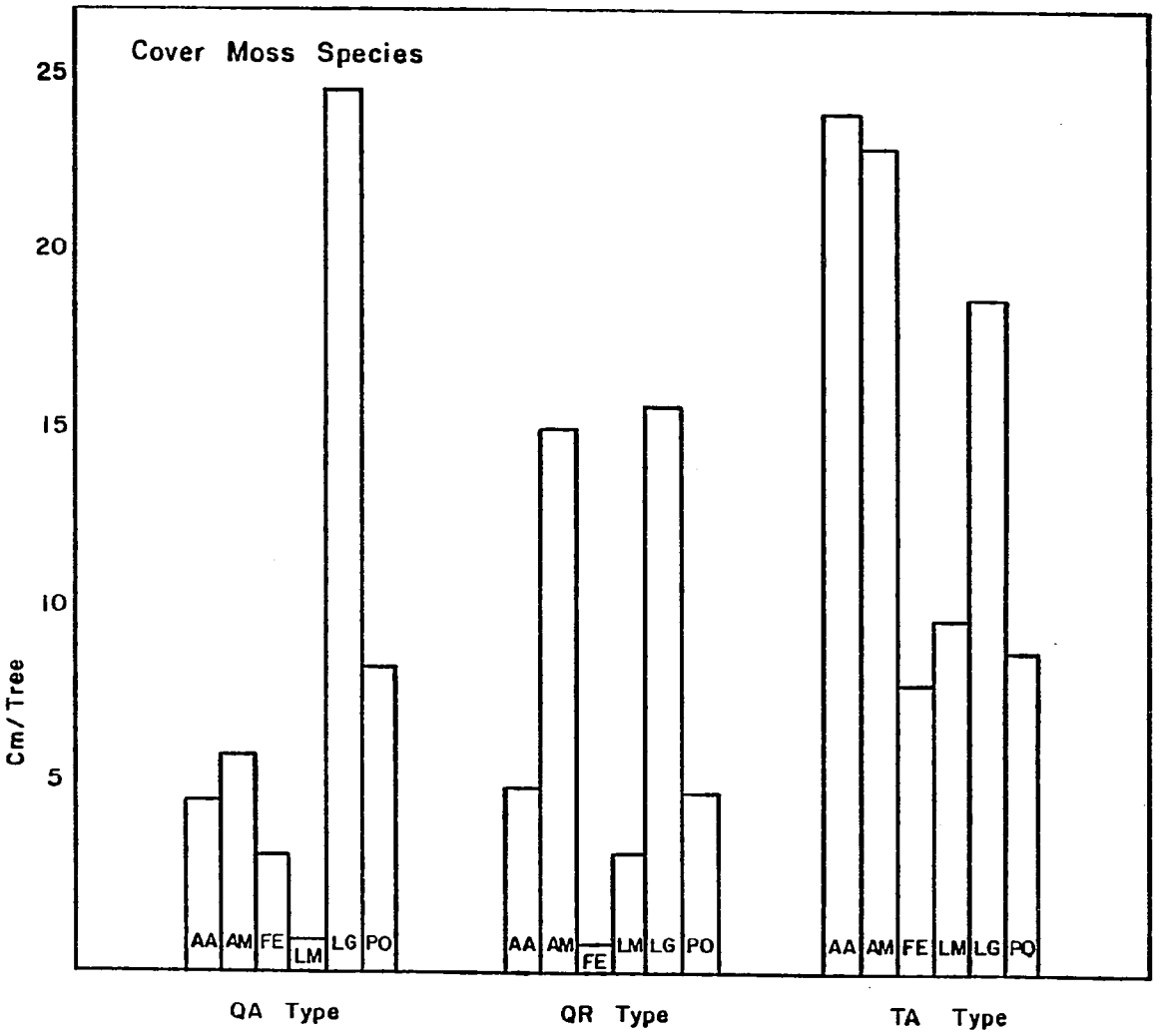
If the cover of epiphytes is compared over vegetation types without regard to the tree species, higher cover and greater richness in the TA type was apparent (Table 9, Figure 4). The cover of most species (17 of 30) was highest in the TA type and cover of the prominent species Anomodon attenuatus, A. minor, A. rostratus, Frullania eboracensis, Graphis scripta and Lepraria membranacea increased markedly in the TA type. A few prominent species, Brachythecium acuminatum, Entodon seductrix and Leskea gracilescens, have highest cover in the QA type. One prominent species,

Table 9. Cover of epiphyte species by type for all trees (cm/tree)

Species	QA Type	QR Type	TA Type
Amblystegium serpens	0.5	0.8	0.5
Anomodon attenuatus	4.8	5.2	24.0
Anomodon minor	6.1	15.2	23.0
Anomodon rostratus	0.4	0.8	4.6
Brachythecium acuminatum	6.8	1.1	1.2
Bryhnia graminicolor			0.1
Campylium hispidulum	0.1	0.1	0.1
Candelaria concolor	0.2	0.4	0.1
Climacium americanum			0.1
Entodon compressus	1.1	4.1	2.8
Entodon seductrix	5.5		
Eurhychium hians			0.1
Fissidens cristatus			0.1
Fissidens subbasilaris			0.1
Frullania eboracensis	3.0	2.5	7.9
Frullania inflata		1.4	0.6
Graphis scripta	0.1	0.3	4.0
Lepraria membranacea	0.8	3.0	9.8
Leskea gracilescens	24.9	15.4	18.6
Lindbergia brachyptera	0.1		0.1
Mnium cuspidatum	0.6	0.1	1.1
Orthotrichum pumilum	0.1	0.2	0.1
Parmelia bolliana	0.1	0.1	0.3
Physcia orbicularis	8.2	4.6	8.6
Platygyrium repens	0.1	1.1	0.1
Porella platyphylla			0.1
Pylaisiella selwynii		0.1	
Taxiphyllum deplanatum		0.1	0.7
Thelia asprella	2.5	0.2	
Tortella humilis			0.1
No. Trees Sampled	60	86	90
Species Richness	20	21	27

Figure 4. Total cover of epiphytes in different vegetation types

AA = Anomodon attenuatus
AM = Anomodon minor
FE = Frullania eboracensis
LM = Lepraria membranacea
LG = Leskea gracilescens
PO = Physcia orbicularis


Cover Moss Species
25
20
15
10
5
Cm/Tree
AA AM FE LM LG PO
QA Type
AA AM FE LM LG PO
QR Type
AA AM FE LM LG PO
TA Type

Entodon compressus has highest cover in the QR type. From examination of the same host species in different vegetation types, the overall increase in the TA type can be attributed primarily to the microclimate.

Differences in tree species abundance and size in the different vegetation types might be expected to influence total epiphyte cover. If this is a dominant influence one would expect that the QR type, should have the highest cover of all types. (Q. rubra was shown to have the highest epiphyte cover and was the dominant tree in the QR type.) However, the total epiphyte cover of the QR type is about half that of the TA type, even though they have roughly the same number of Q. rubra samples (25 in the QR type and 23 in TA type). Species richness also increases in the TA type. A total of 20, 21 and 27 species were found in the QA, QR and TA types respectively.

The average size of trees is somewhat greater in the TA type (Table 10). When the individual species are compared over types the same increase is evident in the TA type (Figure 5). This increase does not match the magnitude of increase in epiphyte cover found in the TA type.

An analysis of the cover by size class shows that the TA type has the highest cover in all size classes except the largest category, in which the QA type has a higher cover (Table 11). Broken down further by tree species, an

Table 10. Diameter breast height (dbh) by tree species and type (ave ± std error)

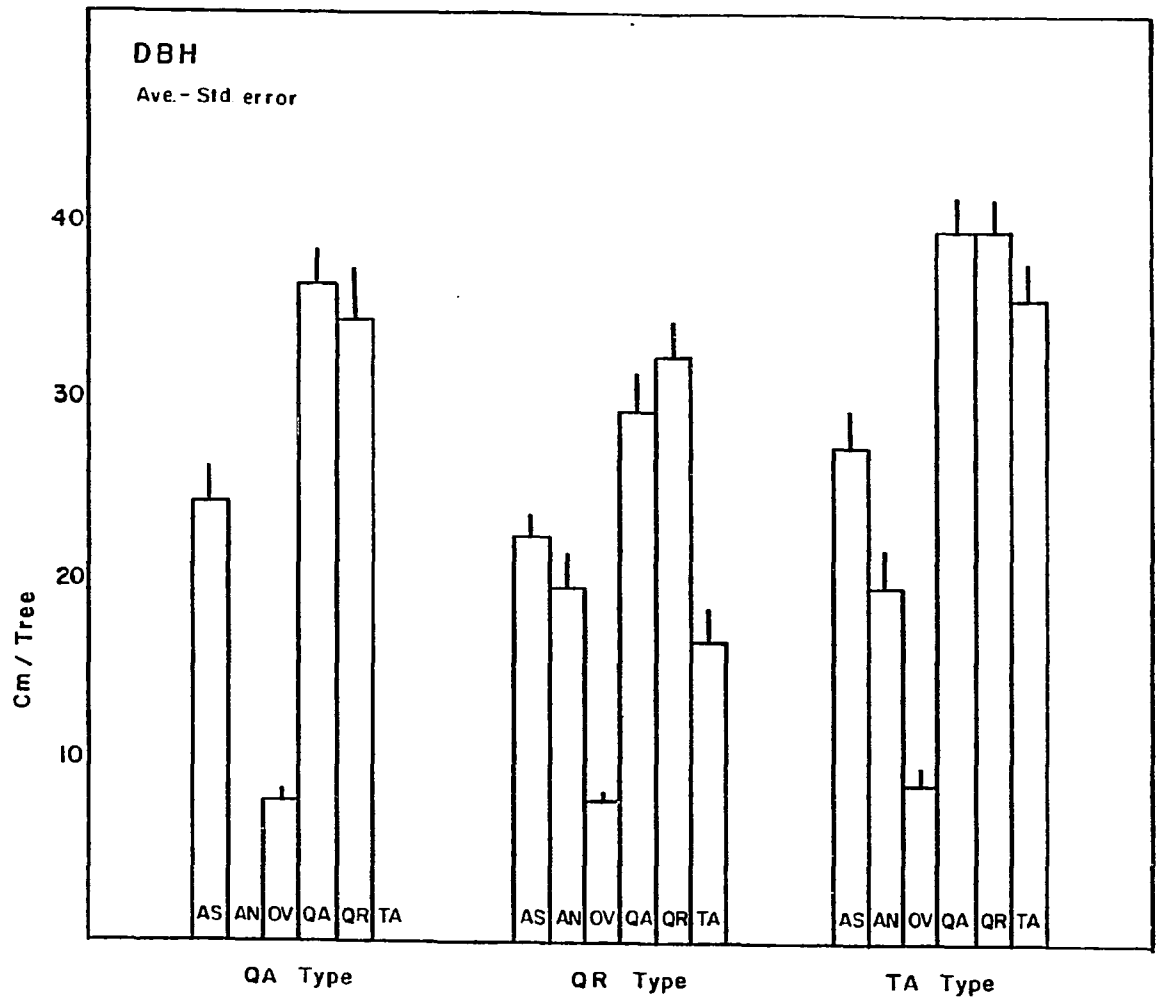
	All Types	QA Type	QR Type	TA Type
All Species	25.2 ± 1.0	24.6 ± 2.1	23.2 ± 1.4	27.6 ± 1.7
AN	20.4 ± 1.3		19.9 ± 2.1	20.9 ± 1.7
OV	8.5 ± 0.3	8.0 ± 0.3	8.4 ± 0.5	9.0 ± 0.5
QA	34.4 ± 1.5	36.9 ± 2.1	30.2 ± 2.3	40.5 ± 1.8
QR	36.2 ± 1.4	35.1 ± 2.8	33.2 ± 2.2	39.9 ± 2.5
TA	33.0 ± 2.4		17.0 ± 2.1	36.2 ± 2.4

Table 11. Cover of mosses in different size classes (ave/tree)

All Species	QA Type	QR Type	TA Type
18 - 23 cm	33.6	69.8	97.9
24 - 29 cm	56.9	85.5	159.4
30 - 35 cm	73.5	59.5	105.6
36 - 40 cm	147.2	121.4	125.9

Figure 5. Average diameter at breast height for six tree species in different vegetation types

AS = All Species
AN = *Acer nigrum*
OV = *Ostrya virginiana*
QA = *Quercus alba*
QR = *Quercus rubra*
TA = *Tilia americana*


DBH
Ave.- Std error
40
30
20
10
Cm / Tree
AS AN OV QA QR TA
AS AN OV QA QR TA
AS AN OV QA QR TA
QA Type
QR Type
TA Type

increase in epiphyte cover is still evident in the TA type (Table 12). One can conclude from this size analysis that the vegetation type has an overriding influence independent of tree size.

Table 12. Cover of mosses for different tree species with dbh held constant (ave./tree)

Species	QA Type (n)	QR Type (n)	TA Type (n)
AN (16 - 17 cm)		7.5 (4)	110.1 (4)
OV (8 cm)	28.5 (5)	11.9 (4)	49.9 (5)
QA (18 - 23 cm)	21.4 (2)	73.5 (5)	
QR (18 - 23 cm)	67.1 (2)	110.2 (4)	139.0 (2)
TA (18 - 23 cm)		11.5 (3)	70.8 (4)

It is often assumed that larger trees have higher cover. There is not, however, a tight correlation between size and cover (Table 13, Figure 6). Except in the QA, type the correlation between size, cover and richness is low. Thus even if the trees were large in the TA type, a corresponding increase in cover would not be expected. The

Table 13. Correlation (r) between dbh, cover and richness for fifteen plots

	DBH-Cover	DBH-Richness	Cover-Richness
All Species All Types	.50*	.37*	.65*
AN	.36	.50*	.87*
OV	.44*	.19	.50*
QA	.50*	.19	.38*
QR	.20	.20	.59*
TA	.21	.20	.63*
QA Type	.71*	.37*	.72*
QR Type	.45*	.42*	.55*
TA Type	.40*	.32*	.56*

*Significant at the .01 level.

high correlation of cover and size in the QA type may be due to the abundance of very large white oaks with high cover of Anomodon minor.

Ostrya was included in this survey specifically for comparison between types, since it occurs abundantly in all types and has a similar size in all types. For the six most abundant epiphytes in the study, the cover on Ostrya increases in the TA type (Table 14). Since the host bark and

Figure 6. Comparison of epiphyte species cover, species richness and dbh for five tree species

AS = All Species
AN = *Acer nigrum*
OV = *Ostrya virginiana*
QA = *Quercus alba*
QR = *Quercus rubra*
TA = *Tilia americana*

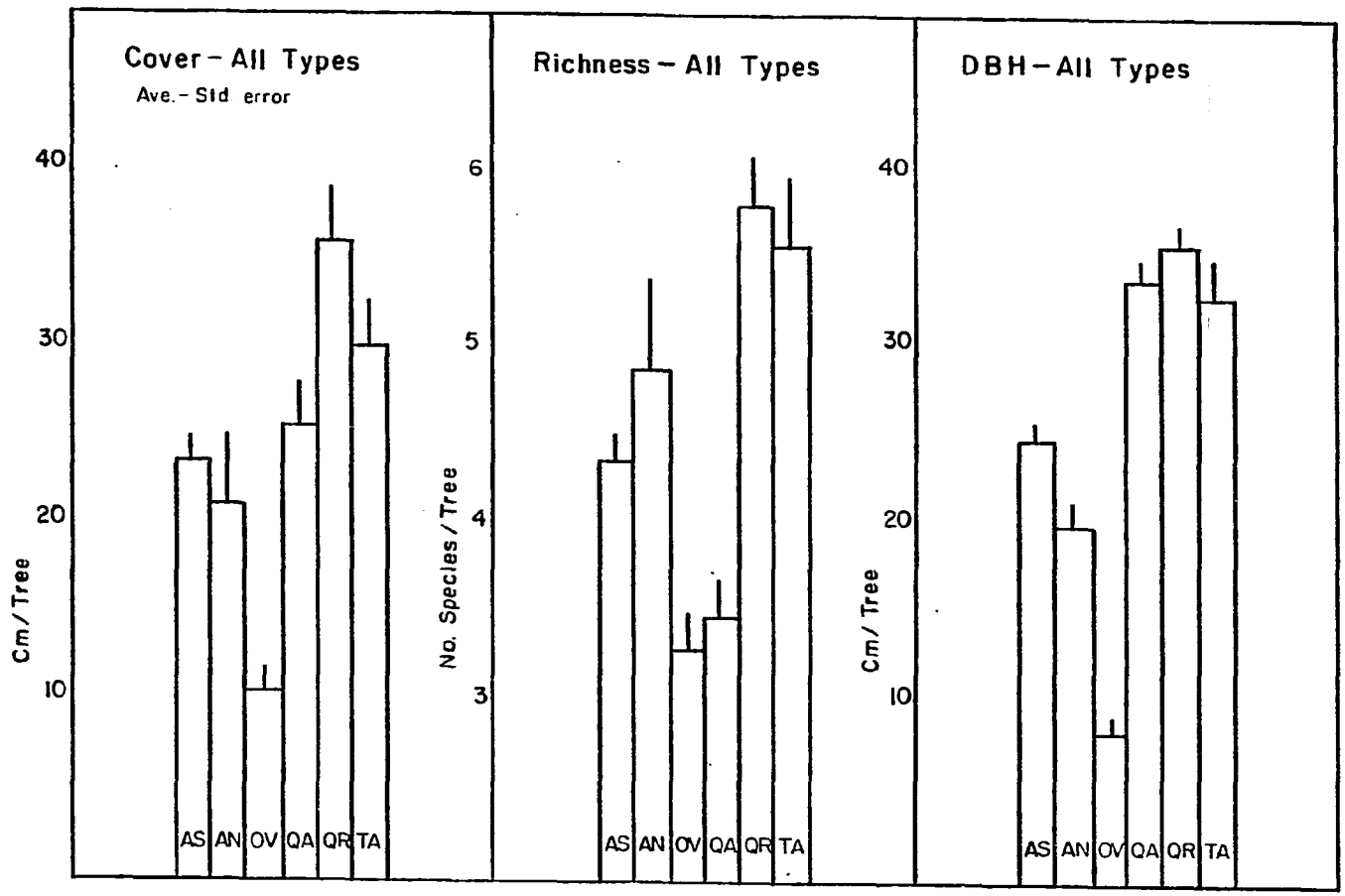

Cover – All Types
Ave. – Std error
Cm / Tree
40
30
20
10
AS AN OV QA QR TA
Richness – All Types
No. Species / Tree
6
5
4
3
AS AN OV QA QR TA
DBH – All Types
Cm / Tree
40
30
20
10
AS AN OV QA QR TA

Table 14. Cover of dominant mosses on Ostrya by type (cm/tree)

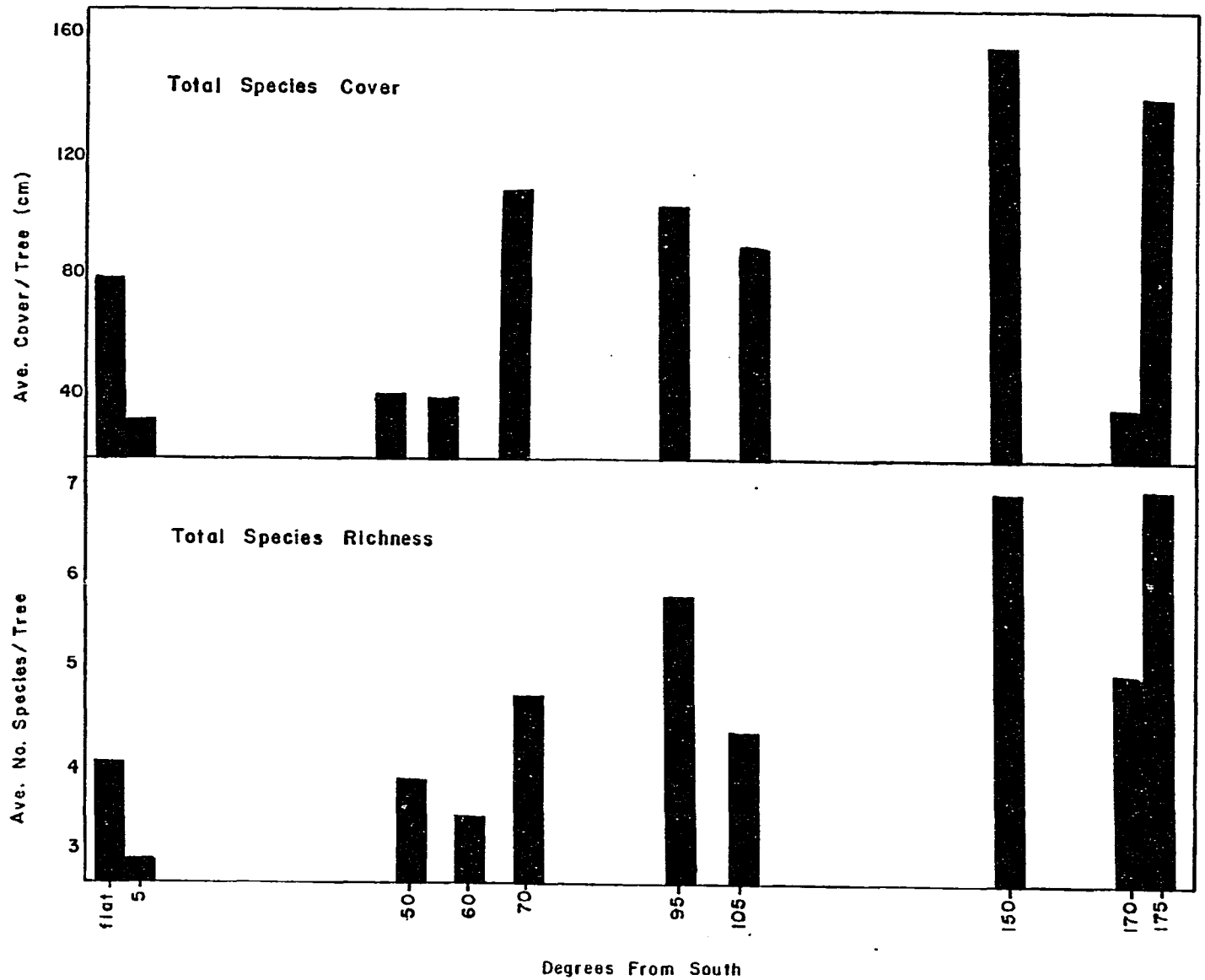
Moss Species	QA Type	QR Type	TA Type
Anomodon attenuatus	0.0	0.0	10.6
Anomodon minor	0.0	9.2	23.2
Frullania eboracensis	0.8	1.3	3.9
Lepraria membranacea	0.0	0.0	0.1
Leskea gracilescnes	7.6	9.3	13.3
Physica orbicularis	6.2	1.8	7.9

size are equal, the microenvironment must account for the different distribution patterns of epiphytes on Ostrya in the different vegetation types.

Though the phorophyte species and size undoubtedly influence distribution to some degree, microclimate is the primary influence on bryophyte distributions in central Iowa. A further analysis of bryophyte distribution through gradient analysis reinforces this conclusion.

Direct gradient analysis was used to ordinate plots along a gradient of aspect (Figure 7), from driest (south-facing) plots to most mesic (north-facing) plots. The average epiphyte cover of all trees sampled within a plot increases from the xeric to the mesic portion of the gradient. Similarly the average species richness increases in the mesic portion of the gradient. This increase in cover and species richness with aspect corresponds to a

Figure 7. Species cover and richness plotted on an aspect gradient


Total Species Cover
Ave. Cover/Tree (cm)
160
120
80
40
Total Species Richness
Ave. No. Species/Tree
7
6
5
4
3
flat
5
50
60
70
95
105
150
170
175
Degrees From South

similar increase in cover and species richness of terricolous bryophytes along the same gradient (see section II).

Detrended correspondence analysis (DCA) produces a two-dimensional ordination on which all the trees are separated (Figure 8). The ordination is based on the epiphyte cover of each tree, so each symbol represents a tree. Rare species were downweighted to obtain the best separation, but no moss species or trees were eliminated from this ordination.

A clear separation of trees on the basis of species is lacking in this ordination. If the phorophyte species is of primary importance to moss distribution then trees of the same species ought to sort out together based on similar epiphyte composition. The ordination of epiphyte species (Figure 9) likewise revealed little evidence for strong host specificity. Only a few epiphytes such as Graphis and Frullania inflata ordinated similarly because of their mutual occurrence on Acer.

In an attempt to determine the gradients represented in this ordination, the vegetation types were projected on to the same ordination. The trees appear to sort according to type (Figure 10). Trees occurring in the TA type sort primarily into the left portion of the ordination. Trees in the QA type are primarily on the right. Trees in the QR

Figure 8. DCA ordination of trees based on cover of epiphytes. Tree species indicated

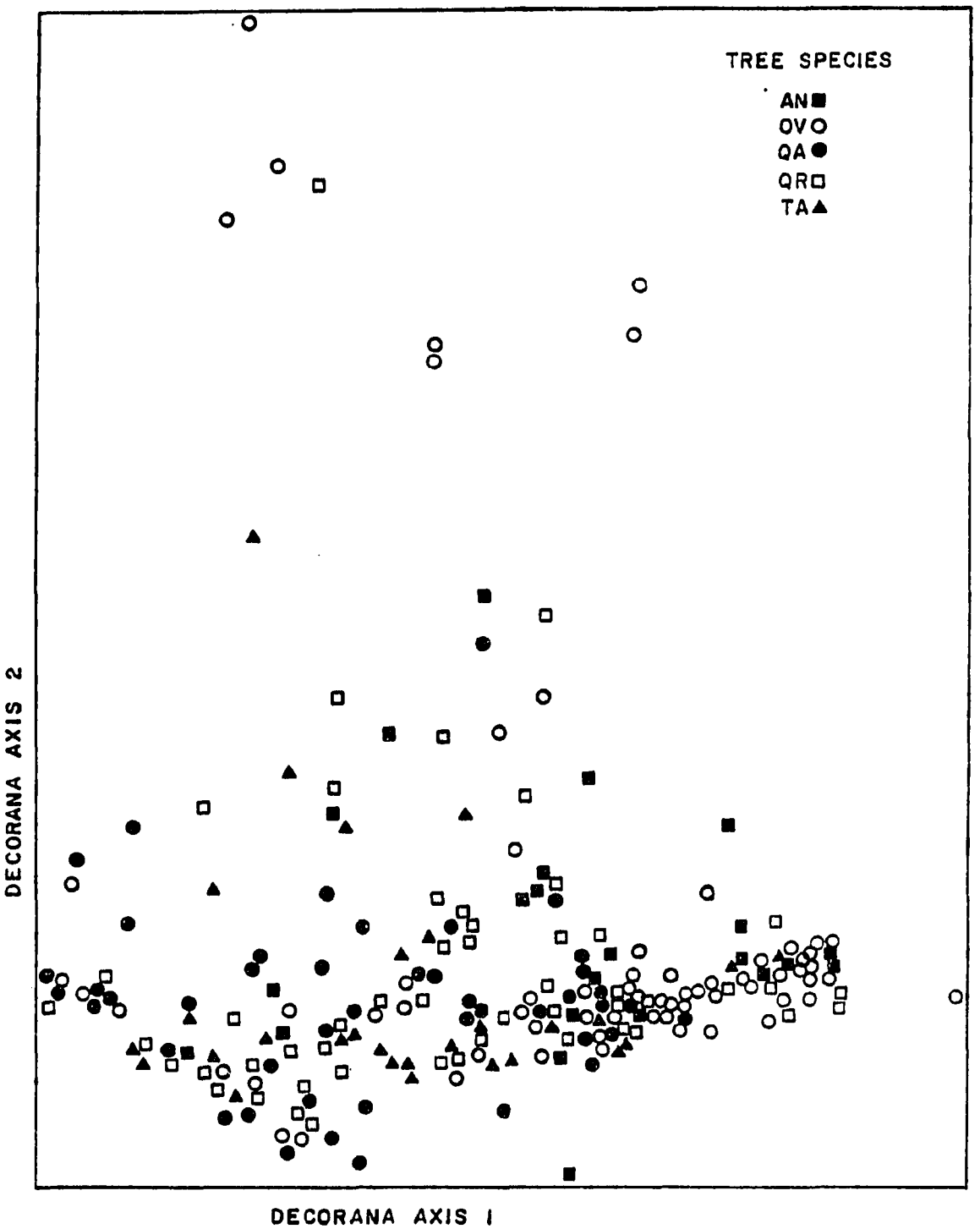

TREE SPECIES
AN
OV
QA
QR
TA
DECORANA AXIS 2
DECORANA AXIS 1

Figure 9. DCA ordination of epiphyte species based on cover on different trees. Epiphyte indicated

As = Amblystegium serpens
Aa = Anomodon attenuatus
Am = Anomodon minor
Ar = Anomodon rostratus
Ba = Brachythecium acuminatum
Bg = Bryhnia graminicolor
Ch = Campylium hispidulum
Cc = Candelaria concolor
Ca = Climacium americanum
Ec = Entodon compressus
Es = Entodon seductrix
Eh = Eurhychium hians
Fc = Fissidens cristatus
Fs = Fissidens subbasilaris
Fe = Frullania eboracensis
Fi = Frullania inflata
Gs = Graphis scripta
Lm = Lepraria membranacea
Lg = Leskea gracilescens
Lb = Lindbergia brachyptera
Mc = Mnium cuspidatum
Op = Orthotrichum pumilum
Pb = Parmelia bolliana
Po = Physcia orbicularis
Pr = Platygyrium repens
Pp = Porella platyphylla
Ps = Pylaisiella selwynii
Td = Taxiphyllum deplanatum
Ta = Thelia asprella
Th = Tortella humilis

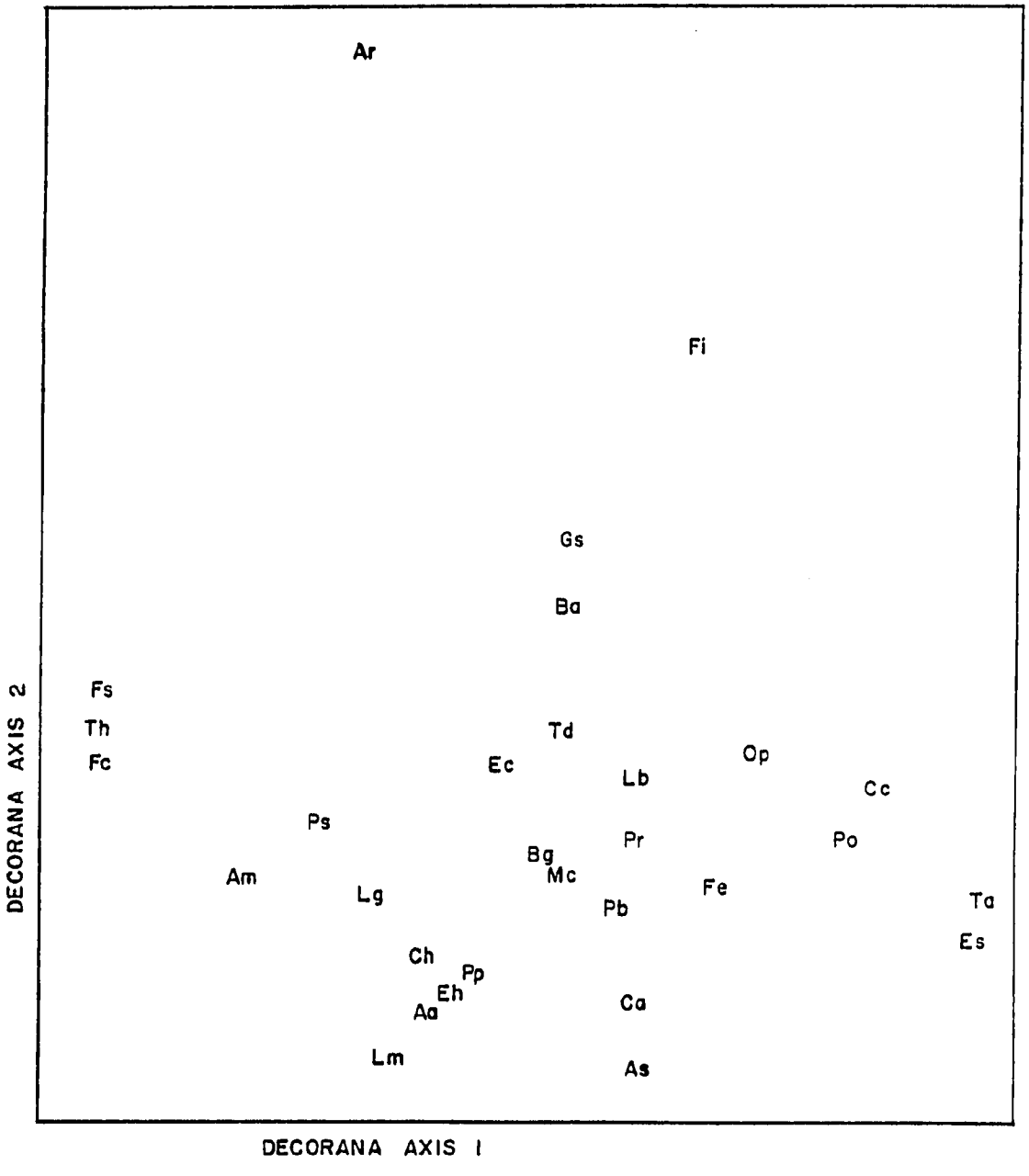
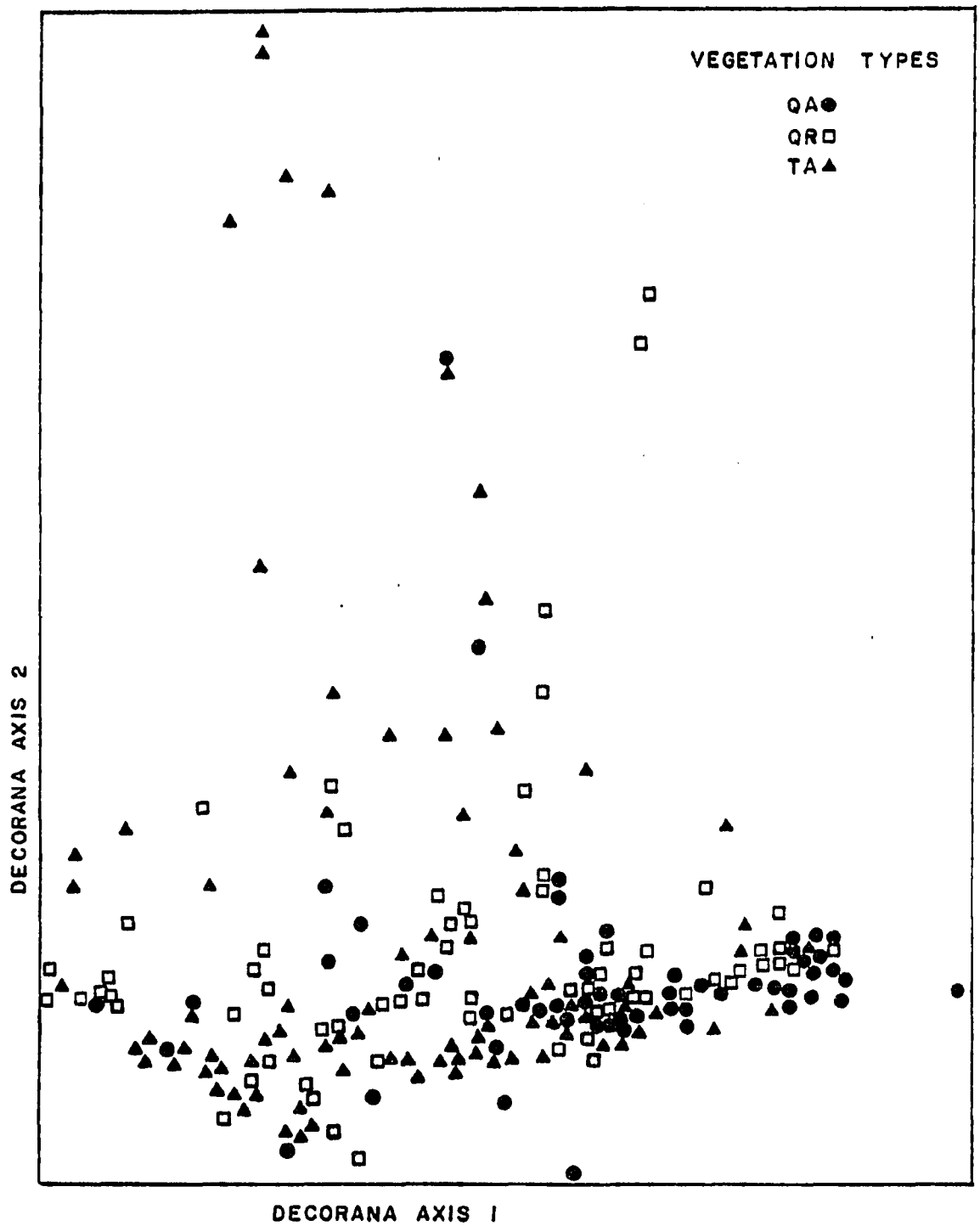

Ar
Fi
Gs
Ba
Fs
Th
Fc
Td
Ec
Op
Lb
Cc
Ps
Pr
Po
Bg
Mc
Am
Lg
Fe
Pb
Ta
Es
Ch
Pp
Eh
Aa
Ca
Lm
As
DECORANA AXIS 2
DECORANA AXIS 1

Figure 10. DCA ordination of trees based on cover of epiphytes. Vegetation type indicated


VEGETATION TYPES
QA●
QR□
TA▲
DECORANA AXIS 2
DECORANA AXIS I

type can be found scattered throughout.

This separation of trees according to the vegetation type is even more evident when only one species at a time is plotted (Figure 11). A similar sorting by vegetation type for Ostrya is shown in Figure 12. This separation is not striking, but it is not expected that it should be because of the contribution of factors such as phorophyte and size. It supports the notion however, that distributions of epiphytes in Iowa are most strongly influenced by the microenvironment.

Figure 11. DCA ordination of trees based on cover of epiphytes. Only Quercus rubra plotted

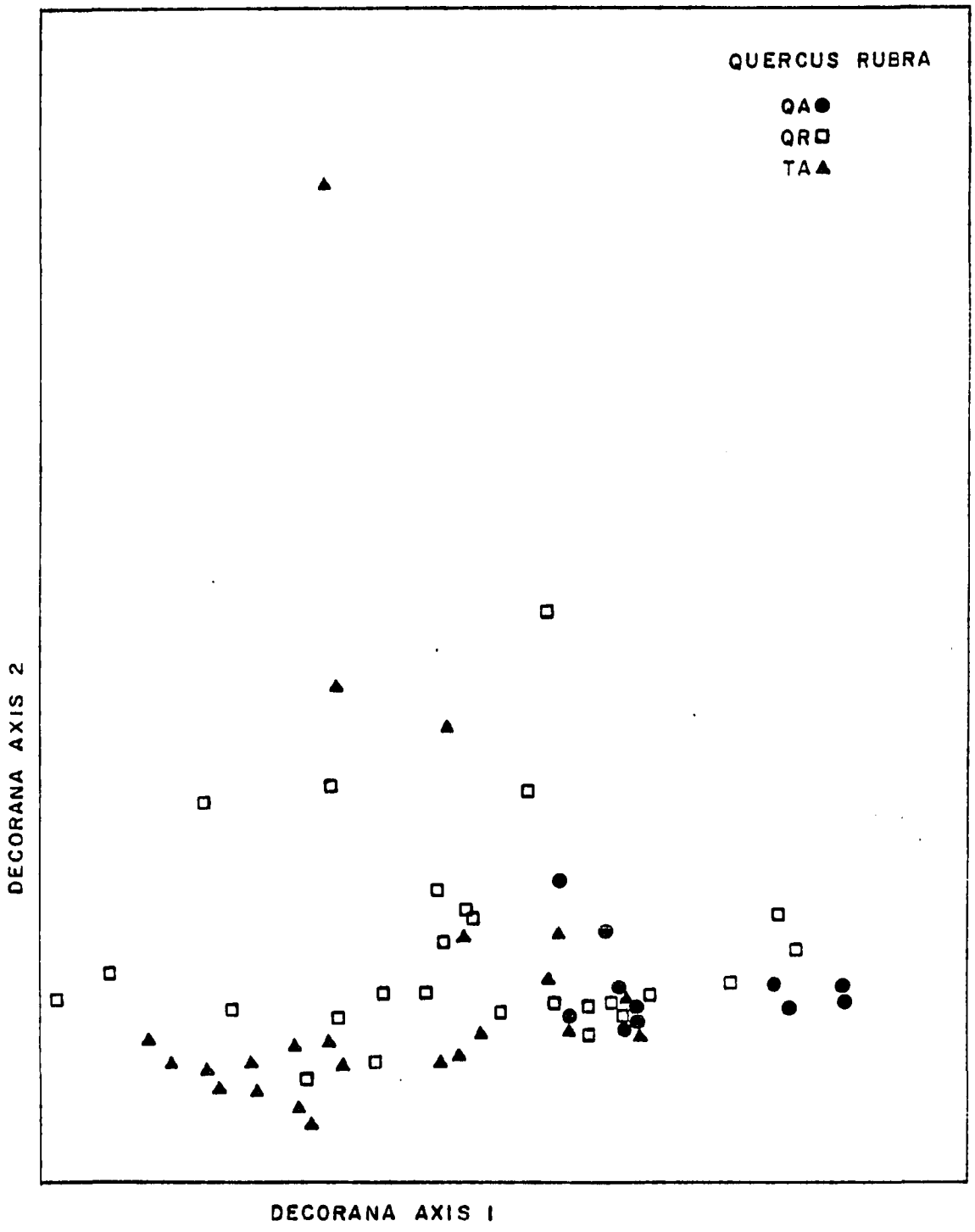
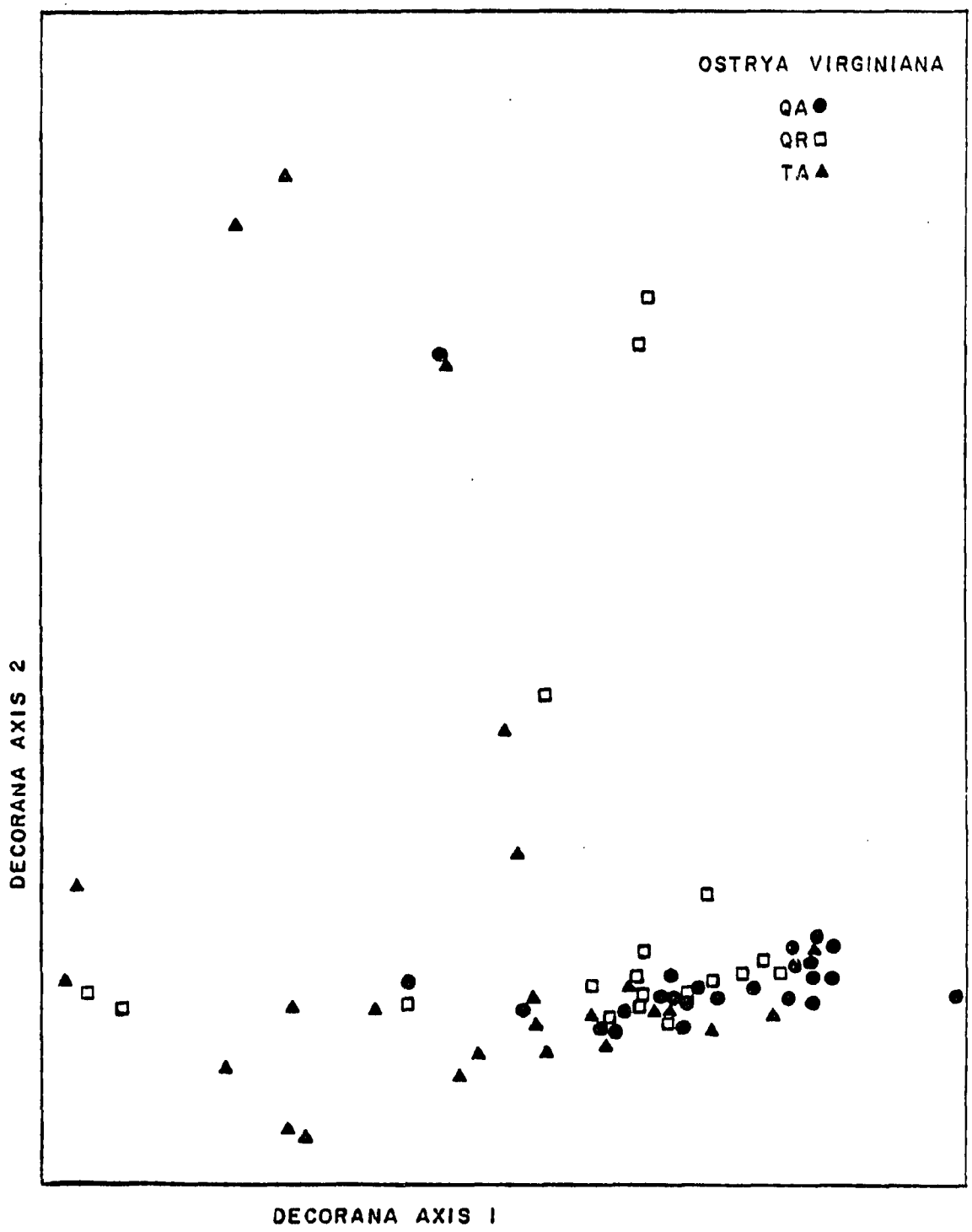

QUERCUS RUBRA
QA
QR
TA
DECORANA AXIS 2
DECORANA AXIS I

Figure 12. DCA ordination of trees based on cover of epiphytes. Only Ostrya virginiana plotted


OSTRYA VIRGINIANA
QA
QR
TA
DECORANA AXIS 2
DECORANA AXIS I

DISCUSSION

The total number of corticolous bryophytes in central Iowa is higher than expected based on extrapolations from studies in the east (Table 15). However, caution must be used in comparing studies, since methods differ as well as the size of the area studied. Of areas studied for epiphytes in the eastern deciduous forest, central Iowa has the lowest species richness. This is expected since the area is farthest west and most xeric. As one moves east there is a notable increase in species richness. Nevertheless the number of epiphyte species in central Iowa (25) is only slightly lower than certain areas to the north (Manitoba, 27) and east (Michigan 30).

Many researchers feel that phorophyte bark characteristics are the most influential factors in determining epiphyte-phorophyte associations within a forest (Culberson, 1955a; Hale, 1955; Barkman, 1958; Beals, 1965; Slack, 1976). Environmental factors are considered secondary in importance. However, most also agree that preference for a single host type is not consistent over the full geographic range of the bryophyte species, even when the same phorophyte is present.

Few of the epiphytes found in central Iowa have been recorded on the same phorophyte species in other studies.

Table 15. Regional comparison of total number of epiphytic bryophytes for the eastern deciduous forests

Study	Site	# Bryophytes	# Mosses	# Hepatics
Johnson-Groh	Central Iowa	25	22	3
Stringer and Stringer (1974)	Southern Manitoba	27		
Hale (1955)	Southern Wisconsin	33		
Culberson (1955a)	Northern Wisconsin	41		
Trynoski and Glime (1982)	Michigan	30	24	6
Phillips (1951)	Michigan	38	30	8
Slack (1976)	Adirondack Mts., NY	36	26	10
Studlar (1982)	Virginia	72	54	18
Palmer (1986)	North Carolina	30	24	6

Species preferring Q. rubra in Michigan included Dicranum scoparium, Hypnum pallescens, Ptilidium pulcherrimum (Trynoski and Glime, 1982), none of which were found in this study. They found no species solely characterized Acer saccharum. In this study A. nigrum was predictably

characterized by Graphis and Frullania eboracensis. Similar comparisons by Trynoski and Glime of their results to Slack's (1976) work confirm that host type alone can not account for the distribution of epiphyte species.

Other comparisons in host preference include Hale's (1955) work in Wisconsin, in which he noted a high cover of Graphis scripta on Acer, consistent with this study. A. saccharum had an average species richness of 1.8 species (Hale, 1955) compared to A. nigrum in this study, which had a average of 4.9 species per tree. Tilia and Q. alba had an average of 3.2 and 4.5 species per tree respectively in Hale's study, compared to 5.6 and 3.5 in this study. (Bryophytes and lichens were included in both studies.) Hale (1955) noted that average species richness for Q. rubra decreased from 8.5 species in maple woods to 4 species in oak woods. Likewise a species richness for Q. rubra of 7.0 and 6.1 were found in the TA and QA types respectively in this study. Hale notes that the lower average species richness in Wisconsin is likely due to the inclusion of many trees with no epiphytes in the prairie-forest region.

Hale (1955) concluded that within a stand, host specificity was most important, but that this "was valid only in small segments of the continuum gradient since the environment of widely separated stands appeared to supercede bark as a limiting factor". It is difficult to know what

Hale considers widely separated stands, but in central Iowa, even between adjacent stands, epiphyte distributions appear to be influenced more by microenvironment than by phorophyte bark and size. Trees of the same species and size have almost twice as much cover in the TA type (north-facing slope) than in the QA type (south-facing slope).

Phillips (1951) concluded that the tree species (bark) is not the most important factor in the development and distribution of corticolous bryophytes in Michigan. He felt that bryophytes were influenced primarily by moisture, and that in habitats with optimum moisture, bryophytes occurred on all tree species in that habitat. For example, Phillips, found that Anomodon minor did not prefer any particular tree species, but was found on trees with ample moisture. It could be found on maple, ironwood and white oak in Michigan. Similarly, in Iowa, Anomodon minor can be found on all phorophytes. Phillips (1951) suggested however, that under dry conditions bryophytes might show a host preference. Iowa is undoubtedly more xeric than Michigan, but no well defined host preference is apparent.

Most of the epiphyte studies in the eastern United States have been conducted over relatively large areas, with no attempt to quantitatively assess the phorophytes across a known microclimatic gradient. Phillip's (1951) stands were scattered throughout Michigan so that microclimate and

macroclimate should be expected to account for differences in moss distributions.

Stringer and Stringer (1974) looked at a smaller area in Manitoba and compared two habitats, bottomland and upland. They found bark to be much less important to bryophytes than to lichens in controlling distributions of epiphytes. They suggest: "macroenvironmental factors, especially shade and humidity, both of which are increased in lowland forests along the river valleys, are of paramount importance in determining the overall distribution of epiphytic bryophyte species. Host substrate factors, such as bark texture, pH and water-holding capacity, probably also play a part in determining individual species distribution and cover, but we consider that macroenvironmental factors have an overriding effect."

The results of Stringer and Stringer come closest to coinciding with the results of this study. They did not, however, sample the same phorophytes in the different habitats to test the effect of microclimate, as was done in this study. The western location in Manitoba places the forest sampled at the western edge of the eastern deciduous forest, corresponding to central Iowa. The similarity in bryophytes, despite differences in trees, is striking.

Leskea gracilescens was one of the dominant species in this study, as well as in Stringer and Stringer's study.

Studies of epiphytes farther east do not make special mention of Leskea, so presumably it has a relatively low cover there. Leskea is found primarily on Q. alba and Tilia in Iowa and on Ulmus americana and Fraxinus pennsylvanica in Manitoba. Other important species in common to both studies include Anomodon minor, Frullania inflata, and Orthotrichum pumilum. Again these species comparisons show the lack of host specificity over broad geographic areas.

It was shown in previous studies on the microclimate and terricolous bryophytes (see Sections I and II) that aspect and resulting microclimate control distribution of vascular plant as well as terricolous bryophytes. North-facing slopes were shown to be cooler and wetter than all other aspects. This cool wet microclimate could account for the higher cover of epiphytes on all phorophytes in the TA type.

A few species, such as Climacium and Bryhnia, which are facultative epiphytes, were encountered only in the TA type (north aspects) in both the corticolous and terricolous survey. The availability of more terricolous species on the north slope may allow more facultative epiphytes to be present. The cover of Anomodon attenuatus, also a facultative epiphyte, is very high on both the ground and trees in the TA type. This mutual high cover can be attributed to the influence of the microclimate associated

with aspect, as well as the availability of spores or propagules.

The question, "does a white oak in a white oak community support the same mosses in the same quantity as a rare white oak in the basswood communities" can be answered at this point. Nine epiphytes can be found on Q. alba in the TA type, whereas 14 were found on Q. alba in the QA type. Species in common to both areas generally had a higher cover in the TA type. A few species tend to be more xerophytic, such as Leskea gracilescens, which had higher cover in the QA type. Fissidens subbasilaris was found only on Q. alba in the TA type, presumably because of the mesic microclimate, and not because of host specificity, since it was not found elsewhere.

Slack (1976) has applied some principles of island biogeography to epiphytes, stating that the trees are similar to islands available for invasion and colonization. It is reasonable to presume that there is no difference in dispersal to maple, oak, basswood or ironwood. Slack maintains that the difference then, is not in dispersal, but in the suitability of the tree (island) for the establishment of particular epiphyte invader, and that tree suitability depends on bark characteristics. That is contrary to the results of this study, which suggest that microclimate is the primary determinant of suitability to

colonization. The rare white oak in the basswood forest is influenced by the microclimate which make it available to species requiring mesic conditions. While oak bark obviously influences this, it is not an overriding factor. Xeric species such as Leskea may be able to get established on Q. alba in mesic sites, but may not persist because of competition with mesic species. Other species such as Anomodon minor (a more mesic species) may be better adapted to these mesic conditions.

The results of this study are contrary to the conclusion of Palmer (1986) that epiphytes segregate along gradients of phorophyte bark. The question Palmer asked, whether the mosses see the forest or the trees, can be answered in favor of the forest, or more specifically the microenvironment. McCune and Antos (1982) also found that epiphytes respond to the microenvironment (stand age, light and moisture). There is little doubt that the phorophyte bark is important, but the difficulty of separating these factors has obscured the importance of microenvironment in determining distributions of bryophytes.

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GENERAL SUMMARY

The relationship of bryophyte and lichen distributions to microclimate and vascular plants in central Iowa forests was examined in the three sections of this dissertation. In the first section, the microclimate analysis, the north slopes were found to have consistently cooler maximum temperature (average of 6^{o} throughout the year) than either south-facing slopes or the uplands. Evaporation was 40% higher on the south-facing slope than the north-facing slope.

In Section II the distribution of terricolous bryophytes was examined, through direct and indirect gradient analysis. Total cover and species richness are highest in the mesic portions of the gradient, corresponding to north-facing aspects. Individual species distributions were examined along the gradient. Anomodon attenuatus was dominant in the mesic portions of the gradient, along with Brachythecium oxycladon, although Brachythecium could be found in high cover in all but the most xeric habitats. Rhychostegium has its highest cover in xeric sites. Fissidens taxifolius had a low but constant cover throughout the gradient.

The correlation of terricolous bryophytes to aspect is apparent in a DECORANA ordination. The gradient expressed

in the ordination is moisture as imposed by aspect. Other gradients such as tree density or percent slope provided no insight into bryophyte distributions.

Terricolous bryophytes comprise a significant proportion of the total ground cover (37%) and diversity (26%) on north aspects. A total of 39 species were found. Species richness was correlated ($r=.55$, $p<.005$) with aspect.

The third section of the dissertation analyzes the relationship of corticolous bryophytes and lichens to the phorophyte and microenvironment. The question "does a rare white oak in a basswood forest have the same bryophytes in the same quantities as a common white oak in a white oak forest" was answered negatively. The epiphytes of a given phorophyte varied with the microenvironment. An average white oak in a basswood forest has a higher total cover of bryophytes and a greater number of species than does a white oak in a white oak forest.

Of the thirty bryophyte and lichen species found, six species account for 80% of the cover. Quercus rubra supported the highest epiphyte cover and species richness of all the trees, and the TA vegetation type supported the highest cover of all three vegetation types.

Cover of epiphytes was shown to be correlated with microclimate. All tree species had higher cover and species richness in the TA type, a north-facing slope community,

than in other vegetation types. The difficulty of separating the influences of tree species (bark type) and microclimate was overcome by sampling the same tree species in different habitats. In this manner bark type was found to be a secondary influence on the distribution of epiphytes.

Comparing this study and the vascular plant study in the same site (Johnson-Groh, 1985), the greatest species richness was found in the herbaceous layer (83 species), followed by the terricolous bryophytes and lichens (39 species), shrubs (35 species), corticolous bryophytes and lichens (30 species) and trees (30 species). Only a few other studies have analyzed vegetation distributions of all layers within the same study plots (Slack, 1977; McCune and Antos, 1981a,b). McCune and Antos (1981a) found the bryoid layer (both terricolous and corticolous layers) to be the most rich in species, followed by the herb, shrub and tree layer. They attribute the high bryophyte diversity to the higher habitat heterogeneity and ability to use a wide array of substrates. The terricolous moss layer in this study included only those on soil; no mosses of rocks or logs were included. Secondly a large number of spring ephemerals were included in the herbaceous count. Spring ephemerals are a phenomenon common to eastern deciduous forests and are lacking in western forest where McCune and Antos conducted

their research. These two factors may explain the difference in order of species richness.

Slack (1977) noted that bryophytes have a higher species richness than vascular plant layers, except at lower elevations where they are equal. In this study species richness was not equal in different layers.

Correlations based on plot cover and species richness between layers was found to be higher for the smaller sized layers (Table 1). The correlations between the terricolous, corticolous and herbaceous layers are much higher than the correlations with the tree layer. This is expected as trees are subject to greater climatic extremes. Smaller layers are buffered from the fluctuations in temperature and moisture. The negative correlation of cover between the trees and bryophytes is interesting and suggests that higher tree cover (shading) inhibits the development of bryophyte communities. Very weak correlations (r^2=<.11) between all layers was found by McCune and Antos (1981b).

The influence of microclimate in central Iowa on the distribution of mosses has been demonstrated for terricolous and corticolous bryophytes. Cover and species richness of both layers respond favorably in mesic north-facing communities. It seems reasonable to assume that bryophyte distributions are influenced by local combinations of plant cover and topography, which also influence local

microclimates, more so than is the vascular vegetation.

Table 1. Correlations based on cover and richness for fifteen plots surveyed for all vegetation layers

	Corticolous	Herbs	Trees
COVER			
Terricolous	.76*	.73*	-.37
Corticolous		.67*	-.25
Herbs			.14
RICHNESS			
Terricolous	.59*	.91*	.48
Corticolous		.62	.55
Herbs			.51

*Significant at the .01 level.

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ACKNOWLEDGMENTS

Special thanks are extended to Dr. Donald Farrar for his help, encouragement and especially for his friendship. I would like to thank Dr. Lois Tiffany for her help with lichen identification and Dr. David Glenn-Lewin for his help with data analysis and both of them for their encouragement and enthusiasm for this project. Judy Shearer and Dr. Eugenia Farrar are thanked for providing some humor during those times when mosses and computers were the enemy rather than the ally. Most of all I would like to thank Dr. Brian L. Groh, a wonderfully patient field assistant and computer consultant, for listening to me, laughing with me and learning with me.

APPENDIX A: NEW COLLECTION RECORDS FOR BOONE COUNTY

Terricolous Species

Amblystegium serpens (Hedw.) BSG

Bryum caespiticium Hedw.

Fissidens taxifolius Hedw.

Gymnostomum aeruginosum Sm.

Mnium marginatum (With) Brid. ex P.-Beauv.

Thuidium delicatulum (Hedw.) BSG

Corticolous Species

Amblystegium serpens (Hedw.) BSG

Fissidens subbasilaris Hedw.

Frullania inflata Gottsche

Orthotrichum pumilum Sw.

Porella platyphylla (L.) Lindb.

Tortella humilis (Hedw.) Jenn.

APPENDIX B: TERRICOLOUS SPECIES COVER BY PLOT AND SPECIES

Cover (Total % cover in 25 m^2 microquadrats/plot)

	Plots			
	1	2	3	4
Amblystegium serpens		30.4		
Amblystegium varium				
Anomodon attenuatus			4.7	
Anomodon minor				
Anomodon rostratus			1.0	
Atrichum undulatum		1.0	0.2	
Aulocomnium heterostichum				
Bartramia pomiformis				
Brachythecium acuminatum				
Brachythecium oxycladon	1.0	19.6	162.5	12.6
Bryhnia graminicolor			30.5	
Bryum caespiticium				
Campylium hispidulum		3.0	3.9	
Chiloscyphus polyanthus				
Cladonia sp.				
Climacium americanum				
Entodon cladorhizans				
Entodon seductrix		2.4		
Eurynchium hians			9.5	
Fissidens cristatus				
Fissidens taxifolius		0.5		1.0
Gymnostomum aeruginosum				
Leskea gracilescens				
Lindbergia brachyptera				
Lophocolea minor				
Mnium affine			27.1	
Mnium cuspidatum		6.0		
Mnium marginatum				
Peltigera canina				
Physcomitrium pyriforme		0.1		
Plagiochilla asplenoides				
Porella platyphylloidea				
Rhodobryum roseum				
Rhychostegium serrulatum		20.8	1.7	5.2
Taxiphyllum deplanatum				5.2
Timmia megapolitana			0.5	
Thelia asperella				
Thuidium delicatulum				
Weissia controversa				
Species Richness	1	9	10	4
Average Cover	0.1	3.4	9.7	1.0

Cover (Total % cover in 25 m^2 microquadrats/plot)

	Plots			
	5	7	8	9
Amblystegium serpens				
Amblystegium varium				
Anomodon attenuatus				
Anomodon minor				
Anomodon rostratus				
Atrichum undulatum				
Aulocomnium heterostichum				
Bartramia pomiformis				
Brachythecium acuminatum				
Brachythecium oxycladon	9.2	13.2	6.0	
Bryhnia graminicolor				
Bryum caespiticium				
Campylium hispidulum		4.3		
Chiloscyphus polyanthus				
Cladonia sp.				
Climacium americanum				
Entodon cladorhizans				
Entodon seductrix				
Eurynchium hians			5.2	
Fissidens cristatus				
Fissidens taxifolius		4.5		
Gymnostomum aeruginosum				
Leskea gracilescens				
Lindbergia brachyptera				
Lophocolea minor				
Mnium affine				
Mnium cuspidatum	1.4	4.8	2.5	
Mnium marginatum				
Peltigera canina				
Physcomitrium pyriforme		1.2		
Plagiochilla asplenoides				
Porella platyphylloidea				
Rhodobryum roseum				
Rhychostegium serrulatum	3.0	12.3	8.5	
Taxiphyllum deplanatum				
Timmia megapolitana				
Thelia asperella				
Thuidium delicatulum				
Weissia controversa		0.2		
Species Richness	3	7	4	0
Average Cover	0.5	1.6	0.8	0.0

Cover (Total % cover in 25 m^2 microquadrats/plot)

	Plots			
	10	11	12	14
Amblystegium serpens	0.2		3.5	
Amblystegium varium				
Anomodon attenuatus				4.5
Anomodon minor				
Anomodon rostratus			0.7	6.4
Atrichum undulatum				2.9
Aulocomnium heterostichum				2.0
Bartramia pomiformis				
Brachythecium acuminatum				
Brachythecium oxycladon			62.1	13.1
Bryhnia graminicolor			1.4	
Bryum caespiticium				
Campylium hispidulum			8.7	4.4
Chiloscyphus polyanthus				
Cladonia sp.				
Climacium americanum				
Entodon cladorhizans				
Entodon seductrix				
Eurynchium hians			77.0	
Fissidens cristatus				
Fissidens taxifolius			1.0	8.6
Gymnostomum aeruginosum				
Leskea gracilescens			0.2	
Lindbergia brachyptera				
Lophocolea minor				
Mnium affine				
Mnium cuspidatum		6.2	12.6	87.9
Mnium marginatum				
Peltigera canina				0.2
Physcomitrium pyriforme				0.8
Plagiochilla asplenoides				
Porella platyphylloidea				
Rhodobryum roseum				
Rhychostegium serrulatum		4.2	68.2	7.3
Taxiphyllum deplanatum			2.0	
Timmia megapolitana				
Thelia asperella				1.0
Thuidium delicatulum				
Weissia controversa				0.2
Species Richness	1	2	11	13
Average Cover	0.1	0.4	9.5	5.6

Cover (Total % cover in 25 m^2 microquadrats/plot)

	Plots			
	15	18	19	24
Amblystegium serpens				2.0
Amblystegium varium	3.6			
Anomodon attenuatus	4.0	105.2	5.0	224.4
Anomodon minor		1.0		
Anomodon rostratus	1.4	16.8	4.5	1.0
Atrichum undulatum	25.2			1.0
Aulocomnium heterostichum				
Bartramia pomiformis				0.2
Brachythecium acuminatum				
Brachythecium oxycladon	7.6	74.2	80.7	134.2
Bryhnia graminicolor			10.6	30.6
Bryum caespiticium				
Campylium hispidulum			0.5	
Chiloscyphus polyanthus				19.5
Cladonia sp.		0.5		6.0
Climacium americanum				13.0
Entodon cladorhizans	0.4	2.0		
Entodon seductrix				
Eurynchium hians	2.8		38.0	
Fissidens cristatus				3.5
Fissidens taxifolius	3.6	0.7		10.8
Gymnostomum aeruginosum				0.1
Leskea gracilescens				
Lindbergia brachyptera				
Lophocolea minor				2.9
Mnium affine		2.1		0.1
Mnium cuspidatum	38.1	35.6	23.9	26.6
Mnium marginatum				8.4
Peltigera canina				3.7
Physcomitrium pyriforme	2.6			
Plagiochilla asplenoides				20.6
Porella platyphylloidea				7.0
Rhodobryum roseum				0.6
Rhychostegium serrulatum	22.6		2.0	
Taxiphyllum deplanatum		2.9		136.5
Timmia megapolitana				3.0
Thelia asperella		0.7		
Thuidium delicatulum		8.2		10.0
Weissia controversa				
Species Richness	11	12	8	24
Average Cover	4.5	10.0	6.6	26.6

Cover (Total % cover in 25 m^2 microquadrats/plot)

	Plots			
	25	26	31	34
Amblystegium serpens	1.9	0.2	1.5	
Amblystegium varium				
Anomodon attenuatus				
Anomodon minor		0.6		
Anomodon rostratus	4.0			
Atrichum undulatum				3.2
Aulocomnium heterostichum				
Bartramia pomiformis				
Brachythecium acuminatum				11.4
Brachythecium oxycladon	2.0			
Bryhnia graminicolor				
Bryum caespiticium	0.6			
Campylium hispidulum	0.1			0.4
Chiloscyphus polyanthus				
Cladonia sp.				
Climacium americanum				
Entodon cladorhizans				
Entodon seductrix				
Eurynchium hians	0.4			30.3
Fissidens cristatus				
Fissidens taxifolius	0.2			
Gymnostomum aeruginosum				
Leskea gracilescens		0.4		
Lindbergia brachyptera				
Lophocolea minor				
Mnium affine				
Mnium cuspidatum	0.4			27.4
Mnium marginatum				
Peltigera canina				
Physcomitrium pyriforme	0.1		0.5	
Plagiochilla asplenoides				
Porella platyphylloidea				
Rhodobryum roseum				
Rhychostegium serrulatum	7.2	5.0	2.0	24.5
Taxiphyllum deplanatum				3.0
Timmia megapolitana				
Thelia asperella				
Thuidium delicatulum				
Weissia controversa	0.1			1.0
Species Richness	11	4	3	8
Average Cover	0.7	0.3	0.2	4.1

Cover (Total % cover in 25 m^2 microquadrats/plot)

	Plots		
	41	45	50
Amblystegium serpens			0.4
Amblystegium varium			
Anomodon attenuatus	201.7		3.7
Anomodon minor			
Anomodon rostratus			
Atrichum undulatum			
Aulocomnium heterostichum			
Bartramia pomiformis			
Brachythecium acuminatum			
Brachythecium oxycladon	77.7		46.8
Bryhnia graminicolor	3.1		
Bryum caespiticium			
Campylium hispidulum			
Chiloscyphus polyanthus			
Cladonia sp.			
Climacium americanum	20.0		
Entodon cladorhizans			
Entodon seductrix			
Eurynchium hians	41.8		43.7
Fissidens cristatus			
Fissidens taxifolius	3.4		3.2
Gymnostomum aeruginosum			
Leskea gracilescens			
Lindbergia brachyptera			0.2
Lophocolea minor			
Mnium affine			8.0
Mnium cuspidatum	43.9		50.9
Mnium marginatum			3.0
Peltigera canina			
Physcomitrium pyriforme			
Plagiochilla asplenoides			
Porella platyphylloidea			
Rhodobryum roseum			
Rhychostegium serrulatum			3.7
Taxiphyllum deplanatum	12.3		5.8
Timmia megapolitana			
Thelia asperella			
Thuidium delicatulum			
Weissia controversa			0.5
Species Richness	8	0	12
Average Cover	16.2	0.0	6.8

APPENDIX C:

TERRICOLOUS SPECIES FREQUENCY BY PLOT AND SPECIES

Frequency (Proportion of 25 microquadrats in which species occur)

	Plots					
	1	2	3	4	5	7
Amblystegium serpens		0.24				
Amblystegium varium						
Anomodon attenuatus			0.24			
Anomodon minor						
Anomodon rostratus			0.04			
Atrichum undulatum		0.04	0.04			
Aulocomnium heterostichum						
Bartramia pomiformis						
Brachythecium acuminatum						
Brachythecium oxycladon	0.04	0.40	0.72	0.36	0.24	0.60
Bryhnia graminicolor			0.36			
Bryum caespiticium						
Campylium hispidulum		0.08	0.40			0.32
Chiloscyphus polyanthus						
Cladonia sp.						
Climacium americanum						
Entodon cladorhizans						
Entodon seductrix	0.12					
Eurynchium hians			0.24			
Fissidens cristatus						
Fissidens taxifolius	0.08			0.04		0.20
Gymnostomum aeruginosum						
Leskea gracilescens						
Lindbergia brachyptera						
Lophocolea minor						
Mnium affine			0.80			
Mnium cuspidatum	0.36				0.12	0.32
Mnium marginatum						
Peltigera canina						
Physcomitrium pyriforme	0.04					0.08
Plagiochilla asplenoides						
Porella platyphylloidea						
Rhodobryum roseum						
Rhychostegium serrulatum	0.52		0.12	0.24	0.12	0.56
Taxiphyllum deplanatum				0.28		
Timmia megapolitana			0.04			
Thelia asperella						
Thuidium delicatulum						
Weissia controversa						0.04

Frequency (Proportion of 25 microquadrats in which species occurs)

	Plots					
	8	9	10	11	12	14
Amblystegium serpens			0.04		0.16	
Amblystegium varium						
Anomodon attenuatus						0.12
Anomodon minor						
Anomodon rostratus					0.16	0.24
Atrichum undulatum						0.20
Aulocomnium heterostichum						0.04
Bartramia pomiformis						
Brachythecium acuminatum						
Brachythecium oxycladon	0.20				0.16	0.32
Bryhnia graminicolor					0.20	
Bryum caespiticium						
Campylium hispidulum					0.16	0.16
Chiloscyphus polyanthus						
Cladonia sp.						
Climacium americanum						
Entodon cladorhizans						
Entodon seductrix						
Eurynchium hians	0.24				0.36	
Fissidens cristatus						
Fissidens taxifolius					0.04	0.32
Gymnostomum aeruginosum						
Leskea gracilescens					0.04	
Lindbergia brachyptera						
Lophocolea minor						
Mnium affine						
Mnium cuspidatum	0.08			0.12	0.20	0.64
Mnium marginatum						
Peltigera canina						0.04
Physcomitrium pyriforme						0.16
Plagiochilla asplenoides						
Porella platyphylloidea						
Rhodobryum roseum						
Rhychostegium serrulatum	0.32			0.04	0.36	0.36
Taxiphyllum deplanatum					0.04	
Timmia megapolitana						
Thelia asperella						0.04
Thuidium delicatulum						
Weissia controversa						0.04

Frequency (Proportion of 25 microquadrats in which species occurs)

	Plots					
	15	18	19	24	25	26
Amblystegium serpens				0.04	0.12	0.04
Amblystegium varium	0.24				0.04	
Anomodon attenuatus	0.04	0.36	0.08	0.84		
Anomodon minor		0.04				0.04
Anomodon rostratus	0.12	0.44	0.12	0.04		
Atrichum undulatum	0.08			0.04		
Aulocomnium heterostichum						
Bartramia pomiformis				0.04		
Brachythecium acuminatum						
Brachythecium oxycladon	0.24	0.52	0.44	0.96	0.08	
Bryhnia graminicolor			0.36	0.56		
Bryum caespiticium					0.08	
Campylium hispidulum			0.04		0.04	
Chiloscyphus polyanthus				0.96		
Cladonia sp.		0.04		0.20		
Climacium americanum				0.12		
Entodon cladorhizans	0.08	0.04				
Entodon seductrix						
Eurynchium hians	0.12		0.40		0.08	
Fissidens cristatus				0.12		
Fissidens taxifolius	0.08	0.04		0.36	0.08	
Gymnostomum aeruginosum				0.12		
Leskea gracilescens						0.04
Lindbergia brachyptera						
Lophocolea minor				0.44		
Mnium affine		0.40		0.08		
Mnium cuspidatum	0.60	0.40	0.32	0.96	0.08	
Mnium marginatum				0.24		
Peltigera canina				0.12		
Physcomitrium pyriforme	0.16				0.08	
Plagiochilla asplenoides				0.24		
Porella platyphylloidea				0.08		
Rhodobryum roseum				0.12		
Rhychostegium serrulatum	0.48		0.08		0.12	0.04
Taxiphyllum deplanatum		0.20		0.44		
Timmia megapolitana				0.08		
Thelia asperella		0.08				
Thuidium delicatulum		0.16		0.16		
Weissia controversa					0.08	

Frequency (Proportion of 25 microquadrats in which species occurs)

	Plots				
	31	34	41	45	50
Amblystegium serpens	0.04				0.08
Amblystegium varium					
Anomodon attenuatus			0.88		0.04
Anomodon minor					
Anomodon rostratus					
Atrichum undulatum		0.12			
Aulocomnium heterostichum					
Bartramia pomiformis					
Brachythecium acuminatum		0.28			
Brachythecium oxycladon			0.76		0.68
Bryhnia graminicolor			0.24		
Bryum caespiticium					
Campylium hispidulum		0.08			
Chiloscyphus polyanthus					
Cladonia sp.					
Climacium americanum			0.28		
Entodon cladorhizans					
Entodon seductrix					
Eurynchium hians		0.72	0.76		0.68
Fissidens cristatus					
Fissidens taxifolius			0.20		0.12
Gymnostomum aeruginosum					
Leskea gracilescens					
Lindbergia brachyptera					0.04
Lophocolea minor					
Mnium affine					0.04
Mnium cuspidatum		0.52	0.88		0.68
Mnium marginatum					0.04
Peltigera canina					
Physcomitrium pyriforme	0.04				
Plagiochilla asplenoides					
Porella platyphylloidea					
Rhodobryum roseum					
Rhychostegium serrulatum	0.04	0.40			0.20
Taxiphyllum deplanatum		0.08	0.48		0.36
Timmia megapolitana					
Thelia asperella					
Thuidium delicatulum					
Weissia controversa		0.04			0.04

APPENDIX D: COVER OF CORTICOLOUS SPECIES FOR ALL TREES

T# = Tree number
TS = Tree species
DBH = Diameter breast height
VT = Vegetation Type
TCOV = Total cover of all epiphytes
BCOV = Total cover of bryophytes
LCOV = Total cover of lichens
TR = Total richness of all epiphytes
BR = Total richness of bryophytes
LR = Total richness of lichens

T#	TS	DBH	VT	TCOV	BCOV	LCOV	TR	BR	LR
1	QA	33	QA	90.4	79.0	11.4	6	4	2
2	QR	38	QA	122.8	88.8	34.0	5	4	1
3	OV	9	QA	21.6	18.2	3.4	3	2	1
4	QA	23	QA	42.8	42.2	0.6	4	3	1
5	OV	11	QA	13.0	11.4	1.6	2	1	1
6	QR	31	QA	144.2	106.4	37.8	7	6	1
7	QA	26	QA	42.8	42.2	0.6	5	4	1
8	OV	8	QA	37.6	5.0	32.6	4	2	2
9	QR	39	QA	226.2	135.6	90.6	5	3	2
10	QA	36	QA	78.4	78.4	0.0	4	4	0
11	OV	8	QA	73.0	61.4	11.6	4	2	2
12	QR	34	QA	58.4	52.6	5.8	3	2	1
13	QA	30	QA	35.0	35.0	0.0	5	5	0
14	OV	11	QA	11.0	0.8	10.2	2	1	1
15	QR	20	QA	64.6	38.6	26.0	5	4	1
16	QR	39	QR	119.6	119.6	0.0	6	6	0
17	QA	26	QR	122.4	122.4	0.0	5	5	0
18	TA	22	QR	18.4	18.4	0.0	4	4	0
19	QR	21	QR	76.8	76.8	0.0	5	5	0
20	QR	28	QR	96.4	96.4	0.0	6	6	0
21	QR	19	QR	29.6	29.6	0.0	6	6	0
22	AN	16	QR	11.6	11.6	0.0	4	4	0
23	QA	27	QR	57.0	57.0	0.0	3	3	0
24	QR	33	QR	104.8	104.8	0.0	4	4	0
25	AN	19	QR	10.2	10.2	0.0	2	2	0
26	QA	18	QR	39.8	39.8	0.0	3	3	0
27	TA	18	QR	12.4	12.4	0.0	1	1	0
28	AN	16	QR	9.0	9.0	0.0	3	3	0
29	AN	15	QR	23.2	23.2	0.0	2	2	0
30	QA	23	QR	76.6	76.6	0.0	4	4	0
31	QA	30	QR	38.2	38.2	0.0	2	2	0
32	OV	9	QR	54.0	54.0	0.0	4	4	0
33	OV	6	QR	7.2	7.2	0.0	1	1	0
34	OV	6	QR	2.2	2.2	0.0	2	2	0
35	OV	6	QR	6.0	6.0	0.0	1	1	0
36	OV	8	QR	19.8	19.8	0.0	5	5	0
37	QR	43	TA	68.8	56.6	12.2	7	5	2
38	AN	24	TA	39.4	28.4	11.0	4	3	1
39	OV	10	TA	13.4	13.2	0.2	3	2	1
40	TA	39	TA	24.0	17.2	6.8	6	5	1
41	QR	50	TA	72.8	39.8	33.0	6	4	2
42	TA	44	TA	115.4	115.4	0.0	4	4	0
43	OV	9	TA	8.4	8.2	0.2	5	4	1
44	AN	16	TA	84.2	26.2	58.0	6	3	3
45	OV	9	TA	12.2	10.8	1.4	8	5	3

T#	TS	DBH	VT	TCOV	BCOV	LCOV	TR	BR	LR
46	TA	41	TA	23.0	22.6	0.4	6	5	1
47	QR	47	TA	30.0	27.6	2.4	6	5	1
48	QR	36	TA	32.4	32.4	0.0	3	3	0
49	TA	49	TA	49.2	48.4	0.8	5	4	1
50	AN	10	TA	6.0	0.0	6.0	2	0	2
51	OV	9	TA	16.4	16.0	0.4	4	2	2
52	TA	37	TA	40.6	37.0	3.6	5	3	2
53	OV	7	TA	12.2	6.2	6.0	5	3	2
54	QR	34	TA	37.8	37.0	0.8	5	4	1
55	QR	32	QR	36.4	36.2	0.2	5	4	1
56	OV	8	QR	22.0	11.6	10.4	2	1	1
57	QA	31	QR	58.4	44.2	14.2	4	3	1
58	OV	7	QR	26.2	24.0	2.2	4	3	1
59	QR	40	QR	56.4	56.2	0.2	3	2	1
60	QA	33	QR	73.6	73.6	0.0	2	2	0
61	OV	11	QR	30.2	30.2	0.0	2	2	0
62	QR	33	QR	52.8	49.8	3.0	4	3	1
63	QA	19	QR	67.6	67.6	0.0	3	3	0
64	QA	29	QR	61.4	61.4	0.0	3	3	0
65	QR	35	QR	21.4	21.4	0.0	2	2	0
66	OV	7	QR	4.8	3.0	1.8	2	1	1
67	QA	33	QR	31.2	31.2	0.0	3	3	0
68	QR	37	QR	53.8	49.6	4.2	3	2	1
69	OV	9	QR	7.4	4.2	3.2	3	2	1
70	QA	21	QA	14.2	14.2	0.0	1	1	0
71	OV	6	QA	0.4	0.4	0.0	2	2	0
72	QA	24	QA	141.8	141.8	0.0	3	3	0
73	OV	7	QA	0.4	0.2	0.2	2	1	1
74	QA	25	QA	16.6	12.4	4.2	4	3	1
75	OV	8	QA	4.0	4.0	0.0	1	1	0
76	QA	33	QA	13.6	13.6	0.0	1	1	0
77	QA	25	QA	35.6	35.6	0.0	3	3	0
78	OV	7	QA	0.0	0.0	0.0	0	0	0
79	OV	8	QA	13.0	7.8	5.2	4	2	2
80	QR	58	QR	26.8	26.8	0.0	4	4	0
81	OV	15	QR	10.4	10.4	0.0	2	2	0
82	AN	42	QR	20.4	20.4	0.0	5	5	0
83	QA	31	QR	118.0	116.6	1.4	5	3	2
84	TA	12	QR	9.4	2.2	7.2	3	2	1
85	OV	8	QR	1.8	0.4	1.4	2	1	1
86	QR	13	QR	4.4	0.4	4.0	4	2	2
87	QA	11	QR	5.0	5.0	0.0	2	2	0
88	TA	21	QR	3.6	0.8	2.8	4	3	1
89	TA	12	QR	8.0	1.2	6.8	3	2	1
90	OV	9	QR	3.4	0.6	2.8	2	1	1

T#	TS	DBH	VT	TCOV	BCOV	LCOV	TR	BR	LR
91	QR	40	QR	81.6	72.8	8.8	5	4	1
92	QR	19	QR	144.2	68.0	76.2	4	3	1
93	OV	14	QR	21.6	19.0	2.6	4	3	1
94	QR	19	QR	190.2	51.0	139.2	5	3	2
95	OV	7	QR	4.6	3.0	1.6	4	3	1
96	QR	62	TA	213.8	119.4	94.4	9	7	2
97	TA	33	TA	119.2	96.2	23.0	6	4	2
98	OV	6	TA	93.8	8.6	85.2	3	2	1
99	AN	30	TA	127.8	79.6	48.2	8	6	2
100	QA	44	TA	233.2	233.2	0.0	5	5	0
101	QA	43	TA	196.8	196.4	0.4	7	6	1
102	AN	19	TA	83.8	7.4	76.4	7	4	3
103	TA	41	TA	66.2	59.0	7.2	6	5	1
104	QR	56	TA	161.8	160.4	1.4	9	8	1
105	OV	7	TA	27.0	26.2	0.8	3	2	1
106	QA	37	TA	62.2	62.2	0.0	2	2	0
107	QR	28	TA	221.6	162.2	59.4	8	5	3
108	TA	31	TA	60.6	42.8	17.8	7	4	3
109	AN	17	TA	63.4	45.8	17.6	7	4	3
110	OV	5	TA	19.8	7.2	12.6	2	1	1
111	OV	5	TA	11.2	6.6	4.6	5	3	2
112	TA	66	TA	98.2	92.6	5.6	5	4	1
113	QR	41	TA	97.6	73.8	23.8	8	5	3
114	AN	15	TA	9.0	8.6	0.4	2	1	1
115	OV	7	TA	49.8	46.4	3.4	6	5	1
116	TA	50	TA	191.6	104.4	87.2	8	5	3
117	OV	9	QR	146.4	146.4	0.0	3	3	0
118	QR	31	QR	51.8	35.6	16.2	3	1	2
119	QA	24	QR	48.8	33.6	15.2	6	4	2
120	OV	7	QR	70.6	65.6	5.0	4	2	2
121	QR	41	QR	210.2	103.4	106.8	4	3	1
122	QA	48	QR	121.8	121.4	0.4	6	5	1
123	QR	39	QR	210.4	210.0	0.4	5	4	1
124	QA	23	QR	81.6	73.4	8.2	4	3	1
125	OV	10	QR	17.6	17.6	0.0	2	2	0
126	AN	28	QR	79.8	54.4	25.4	6	3	3
127	AN	18	QR	112.6	65.2	47.4	4	2	2
128	AN	20	QR	171.6	161.4	10.2	7	4	3
129	OV	7	QR	35.4	33.8	1.6	4	3	1
130	QR	39	QR	194.0	149.6	44.4	6	5	1
131	QA	30	QR	83.0	82.6	0.4	3	2	1
132	OV	6	QR	34.6	27.4	7.2	4	2	2
133	QR	29	QR	180.6	129.8	50.8	8	4	4
134	QA	23	QR	101.8	101.4	0.4	3	2	1
135	QR	40	TA	148.8	97.6	51.2	4	3	1

T#	TS	DBH	VT	TCOV	BCOV	LCOV	TR	BR	LR
136	AN	29	TA	236.0	188.6	147.4	0	8	2
137	OV	11	TA	246.4	246.2	0.2	8	7	1
138	TA	37	TA	226.2	211.2	115.0	0	8	2
139	QR	48	TA	198.0	68.6	129.4	8	7	1
140	AN	26	TA	103.4	58.0	45.4	8	5	3
141	OV	6	TA	44.6	34.2	10.4	5	3	2
142	TA	26	TA	164.8	129.8	35.0	7	6	1
143	TA	33	TA	275.8	263.0	12.8	5	4	1
144	OV	13	TA	136.6	136.6	0.0	5	5	0
145	AN	17	TA	147.0	65.6	81.4	8	5	3
146	QR	37	TA	197.4	140.6	56.8	6	5	1
147	OV	14	TA	205.2	205.2	0.0	6	6	0
148	AN	25	TA	111.2	105.2	6.0	6	3	3
149	QR	23	TA	125.0	107.2	117.8	0	7	3
150	QR	39	TA	179.4	176.0	3.4	7	5	2
151	TA	24	TA	103.2	77.6	25.6	9	7	2
152	OV	8	TA	86.2	79.8	6.4	6	5	1
153	TA	28	TA	163.0	139.6	23.4	7	5	2
154	QA	46	QA	112.2	112.2	0.0	4	4	0
155	OV	7	QA	3.8	0.4	3.4	2	1	1
156	QA	30	QA	44.4	44.4	0.0	3	3	0
157	OV	7	QA	25.0	18.4	6.6	5	3	2
158	QA	41	QA	69.2	69.2	0.0	4	4	0
159	OV	5	QA	5.2	0.4	4.8	2	1	1
160	QA	44	QA	78.2	78.2	0.0	2	2	0
161	OV	9	QA	19.4	18.0	1.4	3	2	1
162	QA	26	QA	47.6	47.6	0.0	3	3	0
163	OV	7	QA	5.0	1.0	4.0	3	2	1
164	QR	40	QR	128.2	127.8	0.4	7	6	1
165	AN	21	QR	40.2	14.4	25.8	5	3	2
166	OV	8	QR	4.0	1.2	2.8	2	1	1
167	QA	43	QR	84.0	83.8	0.2	4	3	1
168	QA	56	QR	35.2	24.6	10.6	5	3	2
169	QA	40	QR	156.4	126.2	30.2	3	2	1
170	AN	16	QR	8.2	3.6	4.6	4	2	2
171	QR	34	QR	43.6	42.4	1.2	3	2	1
172	AN	18	QR	10.8	9.0	1.8	2	1	1
173	QR	48	QR	43.6	41.8	1.8	5	3	2
174	OV	7	QR	1.2	1.0	0.2	2	1	1
175	QA	37	QR	107.6	107.6	0.0	2	2	0
176	QR	26	QR	24.4	23.8	0.6	5	4	1
177	AN	17	QR	1.0	0.0	1.0	1	0	1
178	AN	13	QR	0.8	0.0	0.8	1	0	1
179	QR	38	QR	41.4	33.2	8.2	5	3	2
180	QA	55	QA	217.0	209.8	7.2	5	4	1

T#	TS	DBH	VT	TCOV	BCOV	LCOV	TR	BR	LR
181	OV	10	QA	49.2	37.4	11.8	4	3	1
182	QR	47	QA	162.2	144.6	17.6	5	4	1
183	QA	43	QA	90.6	90.6	0.0	2	2	0
184	OV	9	QA	61.6	59.6	2.0	3	2	1
185	QR	41	QA	258.4	196.6	161.8	0	8	2
186	QR	36	QA	248.2	189.6	158.6	0	6	4
187	QA	47	QA	84.2	84.2	0.0	4	4	0
188	OV	8	QA	36.8	25.6	11.2	3	2	1
189	QR	22	QA	69.6	58.4	11.2	5	3	2
190	QA	60	QA	122.0	121.0	1.0	4	3	1
191	OV	7	QA	11.6	0.2	11.4	3	1	2
192	QA	48	QA	92.4	92.4	0.0	3	3	0
193	OV	8	QA	6.4	0.2	6.2	2	1	1
194	TA	30	TA	137.2	127.4	9.8	6	3	3
195	AN	26	TA	169.4	79.0	90.4	7	3	4
196	OV	11	TA	59.0	59.0	0.0	2	2	0
197	QR	45	TA	158.8	127.8	131.0	1	7	4
198	QR	46	TA	236.6	159.2	77.4	9	5	4
199	TA	36	TA	197.2	99.0	98.2	8	5	3
200	OV	12	TA	69.6	60.2	9.4	5	3	2
201	AN	17	TA	145.8	56.0	89.8	7	4	3
202	TA	45	TA	110.4	102.4	8.0	8	6	2
203	OV	8	TA	42.6	28.4	14.2	7	5	2
204	QR	45	TA	238.0	167.8	70.2	8	4	4
205	QR	39	TA	125.0	86.6	38.4	6	3	3
206	TA	26	TA	258.2	242.0	116.2	0	6	4
207	OV	8	TA	77.0	40.4	36.6	5	3	2
208	OV	11	TA	46.0	36.2	9.8	6	4	2
209	TA	39	TA	211.0	185.0	26.0	5	3	2
210	OV	9	QA	12.6	7.2	5.4	2	1	1
211	QA	45	QA	94.8	92.4	2.4	2	1	1
212	OV	6	QA	8.4	2.8	5.6	2	1	1
213	QA	46	QA	85.4	85.0	0.4	3	2	1
214	OV	7	QA	5.0	0.4	4.6	2	1	1
215	QA	39	QA	39.8	38.8	1.0	2	1	1
216	OV	11	QA	27.0	19.0	8.0	2	1	1
217	QA	37	QA	160.6	150.4	10.2	3	2	1
218	OV	7	QA	45.6	34.4	11.2	2	1	1
219	QA	39	QA	102.8	102.8	0.0	2	2	0
220	QR	43	QA	139.6	123.0	16.6	6	4	2
221	QR	62	TA	109.4	109.0	0.4	5	4	1
222	OV	13	TA	155.0	155.0	0.0	3	3	0
223	QA	38	TA	144.0	144.0	0.0	3	3	0
224	TA	23	TA	66.8	66.4	0.4	3	2	1
225	QR	32	TA	167.4	139.0	28.4	5	4	1

T#	TS	DBH	VT	TCOV	BCOV	LCOV	TR	BR	LR
226	OV	8	TA	23.1	20.3	2.8	4	3	1
227	TA	22	TA	69.2	69.2	0.0	5	5	0
228	OV	12	TA	61.8	61.8	0.0	4	4	0
229	QR	29	TA	126.6	120.0	6.6	7	6	1
230	TA	63	TA	60.2	43.0	17.2	3	2	1
231	OV	8	TA	20.4	20.4	0.0	2	2	0
232	QR	18	TA	154.4	112.4	42.0	5	4	1
233	TA	23	TA	65.6	64.8	0.8	5	4	1
234	TA	20	TA	81.6	57.6	24.0	4	3	1
235	QR	17	TA	115.0	96.0	19.0	8	5	3
236	OV	9	TA	34.0	34.0	0.0	2	2	0